THE INFLUENCE OF ROOKERY TERRAIN
ON POPULATION STRUCTURE, TERRITORIAL BEHAVIOR, AND
BREEDING SUCCESS OF STELLER SEA LIONS
IN THE GULF OF ALASKA

RECOMMENDED:

Chairperson, Advisory Committee

Head, Department of Marine Sciences and Limnology

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

3/8/88
Date

THE INFLUENCE OF ROOKERY TERRAIN ON POPULATION STRUCTURE, TERRITORIAL BEHAVIOR, AND BREEDING SUCCESS OF STELLER SEA LIONS IN THE GULF OF ALASKA

A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Louise N. Smith, B.S.

Fairbanks, Alaska

May 1988

ABSTRACT

The effect of rookery terrain on population structure, territorial behavior and breeding success of Steller sea lions was assessed at two rookeries, in the northern Gulf of Alaska. The sea lions using Sugarloaf and Marmot Islands differed in age structure, juveniles being absent from Sugarloaf but present on Marmot during the breeding season. Territory boundaries of breeding bulls on Sugarloaf were stable, and were unaffected by tides. Territory boundaries on Marmot were unstable, shifting with the tide. Territorial bulls occupied two types of territories on Sugarloaf Island (landlocked and water-access) and three types on Marmot (landlocked, tidal and semiaquatic). The behavior of territorial bulls on Marmot was influenced by tides and presence of juvenile animals. These factors were not important on Sugarloaf. The breeding success of territorial bulls was unaffected by location of territory on Sugarloaf. Territory location was important in the breeding success of Marmot Island bulls.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

Funding for this study was provided by the Alaska Department of Fish and Game under the auspices of the OCSEAP program. Additional funds were provided by the office of the Vice Chancellor for Research and Advanced Studies and the Institute of Marine Science, University of Alaska, Fairbanks. Logistic support was provided by NOAA and the United States Coast Guard.

Many people contributed their ideas, support and friendship throughout the course of this study. I thank Don Calkins, Alaska Department of Fish and Game, for introducing me to "island living," giving me the opportunity to study Steller sea lions and for his encouragement during the initial stages of this study.

Dave Johnson, Gay Browning and Scott Brainard provided companionship and support in the field. They lived with me in isolated and strenuous conditions without complaint and constantly reminded me of the levity of many situations. I especially thank Gay Browning for returning to Alaska and volunteering for a "second stint" during my last field season when funds were low. I thank her for the encouragement and most certainly the laughter.

My committee members Drs. Francis Fay, Howard Feder, John Goering and Ed Murphy reviewed drafts of the thesis, as did Bob Day. Dr. Sam Harbo helped with the sampling design. Dave McGuire provided guidance in data analysis. Don Borchert drafted many of the figures. I am greatly indebted to my major advisor, Dr. "Bud" Fay, for his patience, support and belief in me and this study.

I thank former and present graduate students Ann Hoover, John Sease, Pauline Hayton Gehnrich, Philip Martin, Rick Johnson, Jon Lewis, Lori Quakenbush, Allen Doyle and Bob Day for their stimulating discussions and constant encouragement.

During my years of graduate study I have met many women who have been an inspiration to me in their work and ideals. I especially thank Susan Warner, Joanna Roth, Kate Wedemeyer, Kate Moitoret, Alice Stickney, Dr. Susan Sugai, Judy Sherburne, Ann Tiplady, Shann Weston and Kathy Turco for their friendship, advice and inspiration.

I also thank Sean O'Neil for his encouragement, patience and love throughout the protracted final stages of this thesis.

Finally, I thank my parents for providing the opportunity and giving me the support and confidence to further my education.

INTRODUCTION

The importance of territoriality to the reproductive success of males in polygynous pinnipeds has been well documented in the literature (Peterson and Bartholomew 1967; Peterson 1968; Gentry 1970; LeBoeuf 1974; Miller 1975). The stability of established territories on the breeding grounds and the mechanisms by which these territories are maintained affect the entire social structure of breeding herds of otariids (Miller 1975). A primary requirement for the establishment of territorial behavior in a social system is the defense of a resource or goal, which in the case of polygynous pinnipeds is the access to estrous cows for breeding purposes. Those factors that determine or influence the establishment of territories will eventually affect the males' productivity and social structure of the herd (Bartholomew 1970; Leboeuf 1974). One of several interrelated factors most certainly is the availabilty and distribution of breeding females on the rookery (Sandegren 1970; Edie 1977). Another factor that affects not only the density and distribution of females but also the mechanisms of the males' territoriality is the physiography of the substrate where the territories occur (Gentry 1970; Edie 1977; Gisiner 1985).

The primary hypothesis addressed by this study is that the physiography of the substrate where territories are established has an important influence on territorial stability, and hence affects the variance in reproductive success among male Steller sea lions,

Eumetopias jubatus. Previous studies of sea lions (subfamily Otariinae) and fur seals (subfamily Arctocephalinae) in other areas of the world have suggested that male reproductive success is influenced, in part, by the physical nature of the rookery. The success of otariids in the production and rearing of young may be higher when certain requirements are met by the rookery terrain. It is thought that breeding females select rookery sites based primarily on previous experience, site tenacity, and gregarious attraction to other sea lions (Sandegren 1970; Edie 1977). Males are considered opportunists in that they aggregate where the females reside (Peterson and Bartholomew 1967). Their success in establishing, defending and maintaining a territory on those areas has a major influence on the number of females fertilized by them for production in the following year (Gentry 1970; Gisiner 1985).

The physical nature of the rookery terrain may exert a strong influence on the territorial behavior and reproductive success of Steller sea lion populations in the Gulf of Alaska. In addition, the sex and age structure of individual breeding populations may differ, due to the influence of the rookery substrate. Only a few kilometers of the Alaskan coastline are utilized by the Steller sea lion for breeding purposes. Those sites can be assumed to be the most favorable in relation to the production and survival of the young. It is evident, however, that each site is not equally favorable, for production and survival rates vary widely between and within rookeries (Calkins and Pitcher 1982).

The objectives of this study were to assess the influence of the rookery terrain on the (1) population structure, (2) territorial behavior and (3) breeding success of the Steller sea lion on two physiographically different major rookeries in the Gulf of Alaska. The two rookeries chosen for the location of the study, Sugarloaf Island and Marmot Island, are the largest in the northern gulf and produce approximately 40 percent of the pups in that area annually (Calkins and Pitcher 1977, 1978). Marmot Island, the larger of the two, is the only location in the northern Gulf of Alaska where sea lions breed on sandy beaches. This is in contrast to the boulder and rocky outcrop habitat of Sugarloaf Island, which is typical of other rookeries in the Gulf.

Distribution

The Steller sea lion is the most geographically widespread of all the sea lions. Its range extends around the North Pacific Ocean from northern Japan and the Okhotsk Sea to the Aleutian Islands, Bering Sea and Gulf of Alaska and southward along the western coast of North America to central California. Approximately 250 thousand animals inhabit these waters (Rowley 1929; Nishiwaki and Nagasaki 1960; Kenyon and Rice 1961; Loughlin et al. 1984). Conservative population estimates in the northern Gulf of Alaska at the time of this study ranged from 40 to 50 thousand individuals with approximately 18 thousand pups being produced annually (Calkins and Pitcher 1977, 1978, 1982).

Social Organization

Steller sea lions are highly social, polygynous pinnipeds that come ashore to rest, give birth and breed. The highest concentrations of sea lions on land occur from May to October, with lower numbers and concentrations throughout the remainder of the year. Calkins and Pitcher (1982) define three types of areas (rookeries, haulouts and stopover areas) that sea lions utilize, based on time of year and regularity of use.

Rookeries are those areas on which sea lions congregate each year during the breeding season to give birth and breed. Most of the adult sea lions present on these areas are engaged in behaviors associated with breeding and parturition. Certain sections of a rookery may be used by nonbreeding individuals (mainly males).

Haulout areas are those areas that also are used on a predictable basis. Few, if any, pups are born on these areas, however, and breeding activity is at a minimum. Haulouts may be utilized seasonally or throughout the year. Rookeries may be used as haulouts outside the breeding season.

Stopover areas are those used by low numbers of sea lions on an irregular, nonpredictable basis.

In general, territorial bulls are the first to arrive on rookeries that are not used as haulouts outside the breeding season. They usually arrive in early to mid-May (Sandegren 1970; Gentry 1970; Gisiner 1985; this study) and establish territories on all areas of the rookery that will eventually be utilized by the cows. Displays of territorial behavior (fighting, boundary displays, chasing of juveniles) are at a minimum during this time, and as a result, the territorial boundaries are not well defined (Gentry 1970; Gisiner 1985). Some of these early arriving males may leave their territories and return to sea, presumably to feed, returning to the same area several hours later.

Pregnant and estrus cows begin to arrive on the rookery around mid-May, continuing through mid-June, along with late arriving territorial bulls (Gentry 1970; Gisiner 1985; this study). With the arrival of the females, the territorial bulls become more aggressive. Instances of fighting, boundary displays and antagonistic behavior toward subadults increase during this time, resulting in more clearly defined territorial boundaries. Previous studies have shown that these boundaries follow topographic features of the rookery (Gentry 1970; Gisiner 1985).

Territorial bulls aggressively defend their territories throughout the breeding season by chasing or fighting any male sea lion that crosses the established boundary. Boundaries between neighboring males are maintained by the use of stereotyped behaviors known collectively as

the boundary display (Gentry 1970). Instances of boundary displays are frequent at the beginning of the breeding season and decrease as neighboring bulls become accustomed to one another (Gentry 1970; Gisiner 1985). Boundary displays and fights increase when a bull is replaced or when there are changes in existing boundaries. Boundary changes can occur when a new bull succeeds in establishing a territory among established bulls or when an established bull extends his territory into a neighboring bull's territory.

Breeding bulls generally remain on their territories, without feeding, throughout the breeding season. Gentry (1970) recorded durations of up to 65 days for Steller sea lion males at Ano Nuevo Island. During periods of hot weather, bulls may briefly abandon their territory for the sea, for thermoregulatory purposes.

Territorial bulls begin to leave their territories permanently by early to mid-July. These males either leave voluntarily or are forced out by "post season territorial bulls" (Gisiner 1985). Virtually all of the bulls that occupied territories during the breeding season have departed by late July. Although post season territorial bulls may occupy territories that contain cows and pups, they do not aggressively defend their territories, nor do they usually copulate. These males often abandon their territories after a few days to a few weeks and are replaced by successively younger and less experienced males. Territorial boundaries tend to be poorly defined, and territory size

increases during this time (Gentry 1970; Gisiner 1985). By the end of August, the males have dispersed from the rookery and do not return again until the next breeding season. Cows, pups and juveniles may remain on the rookery throughout the fall, utilizing it as a haulout area.

In the northern Gulf of Alaska, pupping commences around mid-May and continues through mid-July, with a peak between 20-25 June (Calkins and Pitcher 1982). Pregnant cows arrive on the rookery about 3 days prior to giving birth (Sandegren 1970) and undergo a brief estrus 12-14 days pospartum (Sandegren 1970; Gentry 1970).

Pregnant cows choose as preferred pupping sites those areas of the rookery that are protected from waves and tides, the most suitable sites being occupied by the more dominant (older) females (Sandegren 1970; Edie 1977). As more females arrive on the rookery, all available areas that are suitable for pupping are occupied by pregnant or parturient females and their pups. Other areas that are too exposed or otherwise unsuitable for pupping are occupied by juveniles or nonbreeding bulls, or they remain vacant (Gentry 1970; this study).

Steller sea lion cows generally copulate only once; 5-15 percent copulate twice (Sandegren 1970; Gentry 1970; Gisiner 1985). Copulations usually take place just before or just after the cow's first postpartum feeding trip to sea (Sandegren 1970; Gentry 1970). Females remain with their pup for about nine days (range 5-13 days) before departing on

their first feeding trip (Sandegren 1970). Thereafter, parturient females leave the rookery approximately every other day on feeding trips that generally do not exceed 24 hours (Sandegren 1970). Pups begin to swim approximately four weeks after birth and begin to accompany the female on successively longer swimming trips, soon therafter (Sandegren 1970).

Previous Studies

Most of the research on the Steller sea lion before 1960 concentrated on feeding habits, body growth and population size with only cursory behavioral information being collected (Scheffer 1945; Wilke and Kenyon 1952; Mathisen 1959; Tikhomirov 1959; Fiscus 1961; Pike 1961; Kenyon and Rice 1961; Kenyon 1962; Mathisen et al. 1962; Thorsteinson and Lensink 1962; Spalding 1964; Tikhomirov 1964a, 1964b; Fiscus and Baines 1966). Not until Orr and Poulter (1967) studied the reproductive and social behavior of the Steller sea lion at Ano Nuevo Island (from 1961-1966) was any quantitative behavioral information on this sea lion collected. Since that time, several studies have been completed concerning aspects of the social behavior of Eumetopias.

Gentry (1970) examined the reproductive and territorial behavior of Steller sea lion bulls at Ano Nuevo Island off the central California coast, continuing the work initiated there by Orr and Poulter (1967) in

the early 1960's. Sandegren (1970) investigated the maternal and breeding behavior of Eumetopias on Lewis Island in the Gulf of Alaska. The behavior of cows and their movements on the rookery were investigated by Edie (1977) on an island near Cape St. James, British Columbia. Gisiner (1985) has recently completed another study of the territorial behavior of Steller sea lion bulls at Ano Nuevo Island, with comparative data collected at Marmot Island in the Gulf of Alaska.

STUDY AREA

The study areas of Sugarloaf and Marmot Islands are located in the geographical center of the breeding Steller sea lion population in the northern Gulf of Alaska. These rookeries are also the largest with respect to pup production, producing approximately 40 percent of the total number of pups born in the northern gulf annually (Calkins and Pitcher 1982).

Sugarloaf Island

Sugarloaf Island, 58 53' 29"N, 152 02' 21"W, is the southernmost island in the Barren Island group, located approximately 32 km southwest of the Kenai Peninsula, Alaska. This island group forms the division between Kennedy Entrance and Stevenson Entrance to Cook Inlet and

Shelikof Strait from the Gulf of Alaska (Fig. 1).

There are seven named islands in the Barren Islands, which range in size from 10 ha to 2,807 ha. The vegetative community that dominates most of the islands is of a grass-sedge type; Ushagat Island is exceptional in being primarily of an alpine-tundra type (Manuwal 1977). Sitka spruce also grows only on Ushagat, the remaining six islands being devoid of trees. A detailed vegetative discussion of the Barren Islands can be found in Bailey (1976).

The Barren Island area is known for severe winds and strong tidal currents. There is also a wide fluctuation in tidal heights. During the 1978, 1979 and 1980 field seasons, tides ranged from lows of -1.37 m to highs of 5.03 m (corrected).

Sugarloaf Island is approximately 81 ha. in size. It reaches a height of 369 m, with steep grass-covered slopes predominating on all sides. Large boulders, rock outcrops and cliffs dominate the coastline, providing suitable haulout and pupping areas for sea lions. The island dropped about 1.5 m in elevation in the 1964 earthquake (Vania and Klinkhart 1967).

Sugarloaf Island supports a wide variety of nesting birds. An extensive study of the marine bird populations in the Barren Islands can be found in Manuwal (1977) and Bailey (1976). Land mammals are not known to reside on Sugarloaf Island. River otters (Lutra canadensis),

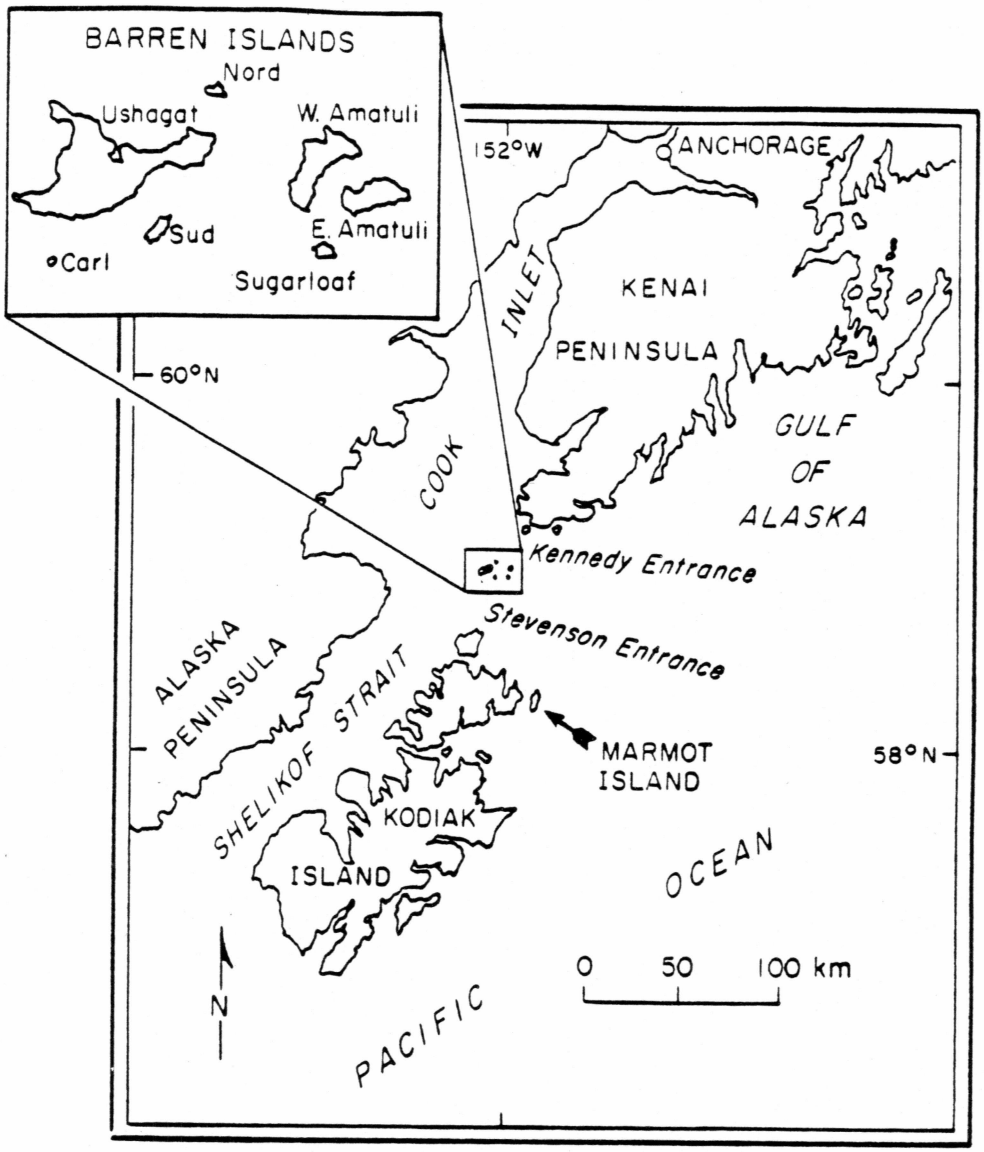

Figure 1. Location map of Sugarloaf Island and Marmot Island.

voles (Cricetidae), marmots (Marmota caligata), ground squirrels (Spermophilus parryi) and arctic foxes (Alopex lagopus) occur on some of the other islands.

Other marine mammals, besides sea lions, that were sighted during this study in the waters around the Barren Islands include: Gray whales (Eschrichtius robustus) in migration during April and May, sea otters (Enhydra lutris), humpback whales (Megaptera novaeangliae), minke whales (Balaenoptera acutorostrata), fin whales (Balaenoptera physalus), killer whales (Orcinus orca), Dall's porpoises (Phocoenoides dalli) and harbor seals (Phoca vitulina). Harbor seals were observed hauling out on the northwest beach of Sud Island. During the latter part of June and early July, northern fur seals (Callorhinus ursinus) were observed hauling out on the northeast end of Sugarloaf Island.

To facilitate the study of sea lions on Sugarloaf Island, I marked off the coast of the island into 13 separate areas based on natural boundaries that occurred at irregular intervals along the shoreline (Fig. 2). These areas were numbered consecutively, starting at the extreme southwestern corner of the island and continuing along the western, northern and northeastern sides. The southern and eastern sides of the island, as well as two large rocks to the south of the island, were not included in the study area due to the poor access and limited visibility of these areas.

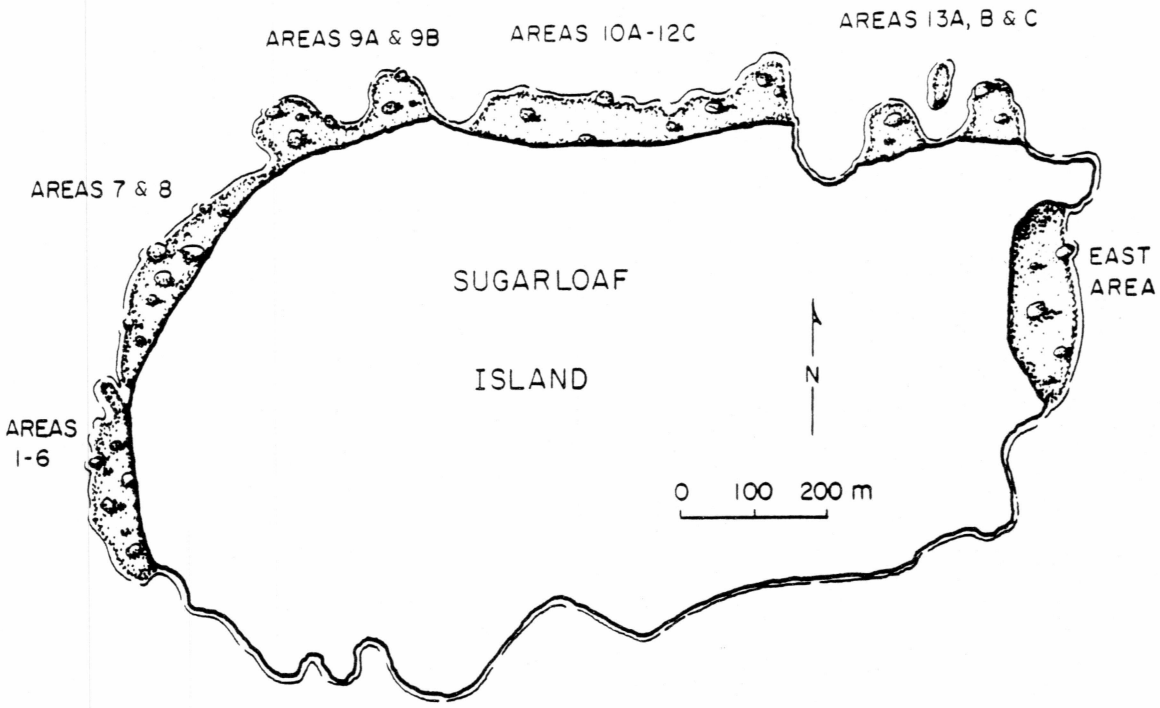

Figure 2. Map of Sugarloaf Island showing designated areas used for the population study 1978-1980.

Population information was collected on each of the 13 designated areas. The behavioral portion of the Sugarloaf Island study was conducted on Area 5, located on the western side of the island. Area 5 is bordered by water on three sides and is connected to the island on the fourth side (Fig. 3). It is composed of a large rock mass measuring approximately 2800 m . Distinct breaks and uplifts characterize the surface of the area. Observations were made from a blind located just east of the area, approximately 35 m up the west slope of the island.

Marmot Island

Marmot Island, 58 N, 152 W, is located approximately 64 km south of Sugarloaf Island, off the eastern side of Afognak Island in the Kodiak Archipelago (Fig. 1). It is approximately 3800 ha. in size and reaches a height of 385 m. The island is characterized by steep-sided valleys and wide ridges with numerous streams and small ponds. The vegetation is dominated by Sitka spruce at lower elevations and alpine meadows along the ridgetops.

The coastline of Marmot Island consists of cobble and sand beaches interspersed with rock outcrops. The shoreline along the east side of the island from its midpoint to the southern end is backed by cliffs ranging in height from 50 m to 1,100 m. These eastern beaches and outcrops are the only areas of the island utilized by sea lions for

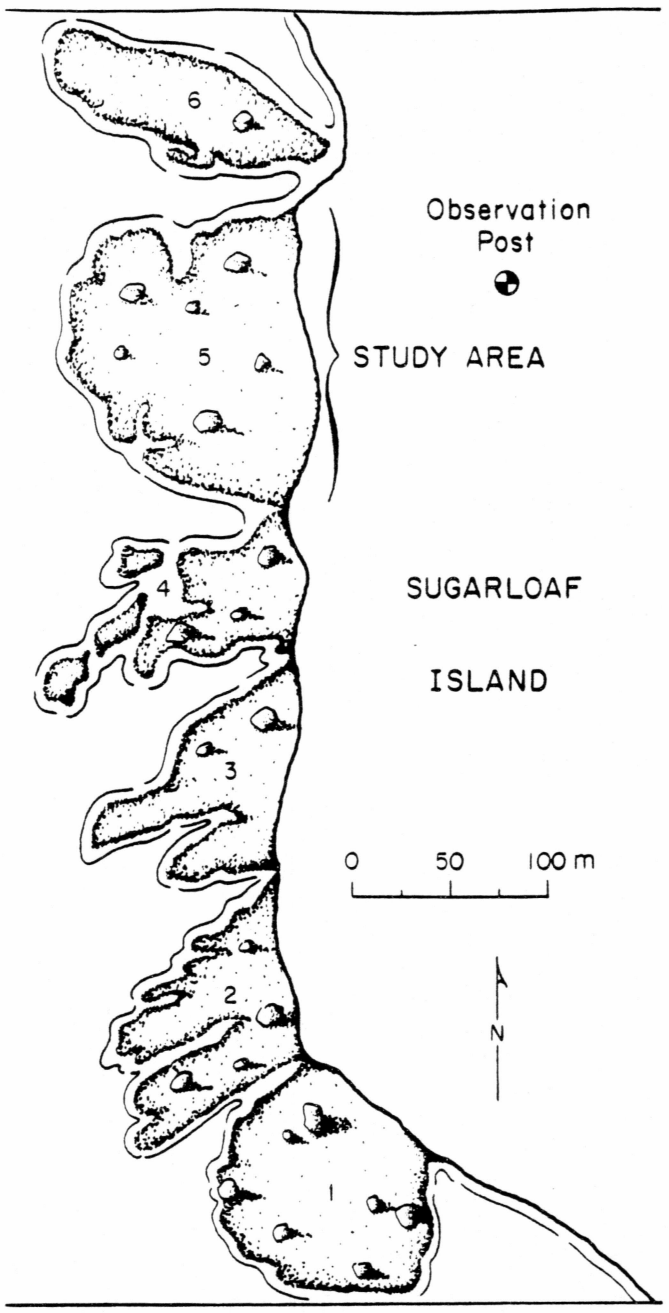

Figure 3. Map of the western shore of Sugarloaf Island, showing the study area (Area 5) used for the behavioral study in 1980.

breeding purposes.

Marmot Island and the surrounding waters support a variety of passerine, raptorial and marine birds. Resident land mammals include river otters, ground squirrels, Sitka black-tailed deer (Odocoileus hemionus) and red fox (Vulpes vulpes). Cattle were introduced onto the island in the 1920's and have since gone feral. In 1985 pigs also were introduced onto the island.

Sea lions are the most numerous marine mammals in the waters surrounding Marmot Island. Other marine mammals sighted there during this study include sea otters, harbor seals and gray whales.

Tidal fluctuations at Marmot Island ranged from -0.82 m to 3.62 m (corrected) during the 1981 field season.

The beaches of Marmot Island were numbered by Alaska Department of Fish and Game biologists during a sea lion study conducted there in 1979 (ADF&G unpublished data). The beaches were numbered from 1 to 7, starting with the most northern beach that was consistently used by the sea lions and continuing southward along the eastern shore of the island (Fig. 4).

Beach 3 was the location of the behavioral part of this study conducted on Marmot Island in 1981. I chose this beach for the study site because of its accessibility and consistent use by large numbers of sea lions. It is a flat, sandy beach, bordered on its northern and

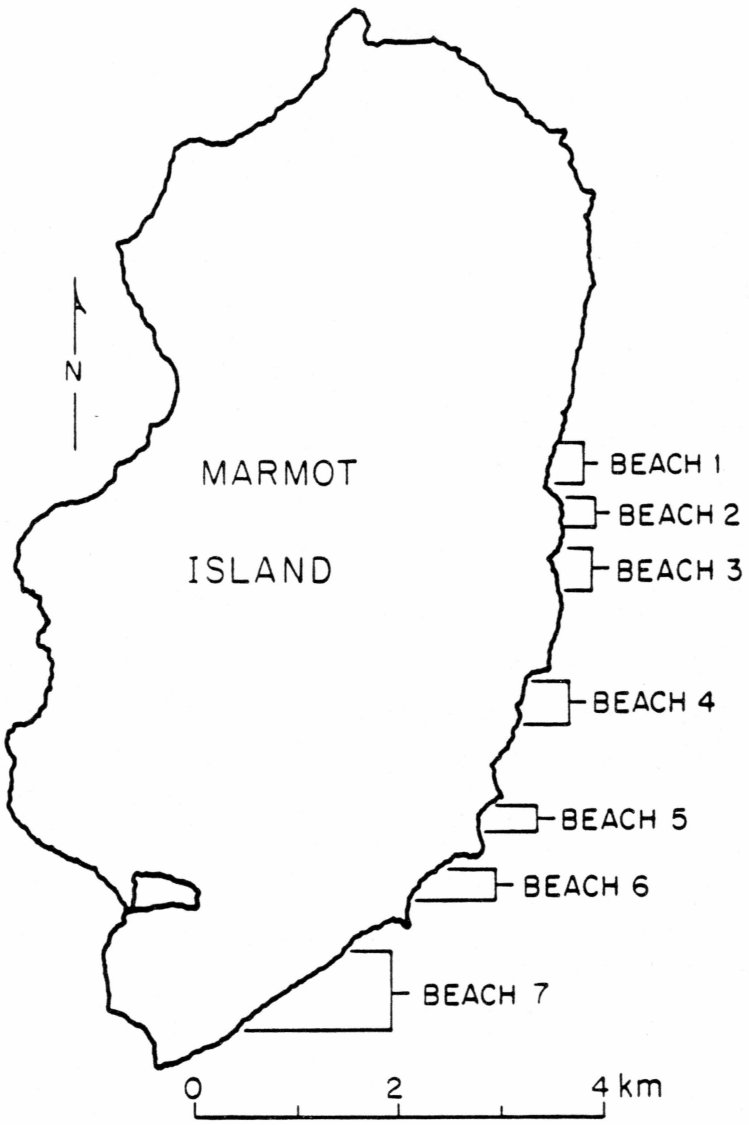

Figure 4. Map of Marmot Island showing designated beaches (adapted from Aumiller, ADF&G unpubl. data).

southern ends by large rock outcrops (Fig. 5). The entire length of the beach is backed by a cliff ranging from 55 to 100 m in height.

Beach 3 was not entirely visible from any one vantage point, therefore I chose to limit the study site to the portion that was visible from the best observation post from which I could positively identify individual animals. That observation post was located 15 m above the middle portion of Beach 3 on a small (1 m) rock outcrop on the cliff to the west of the beach. The study site was approximately 135 m in length and varied in width with the tide from approximately 30 m at high tide to 100 m at low tide.

METHODS

Population information was collected on Sugarloaf Island in 1978, 1979 and 1980. Behavioral information also was collected during this time. A detailed behavioral study was conducted on Marmot Island in 1981. During the 1979 field season on Sugarloaf Island, a concurrent population study was being conducted on Marmot Island by Alaska Department of Fish and Game biologists, and some of the data from that study are included here.

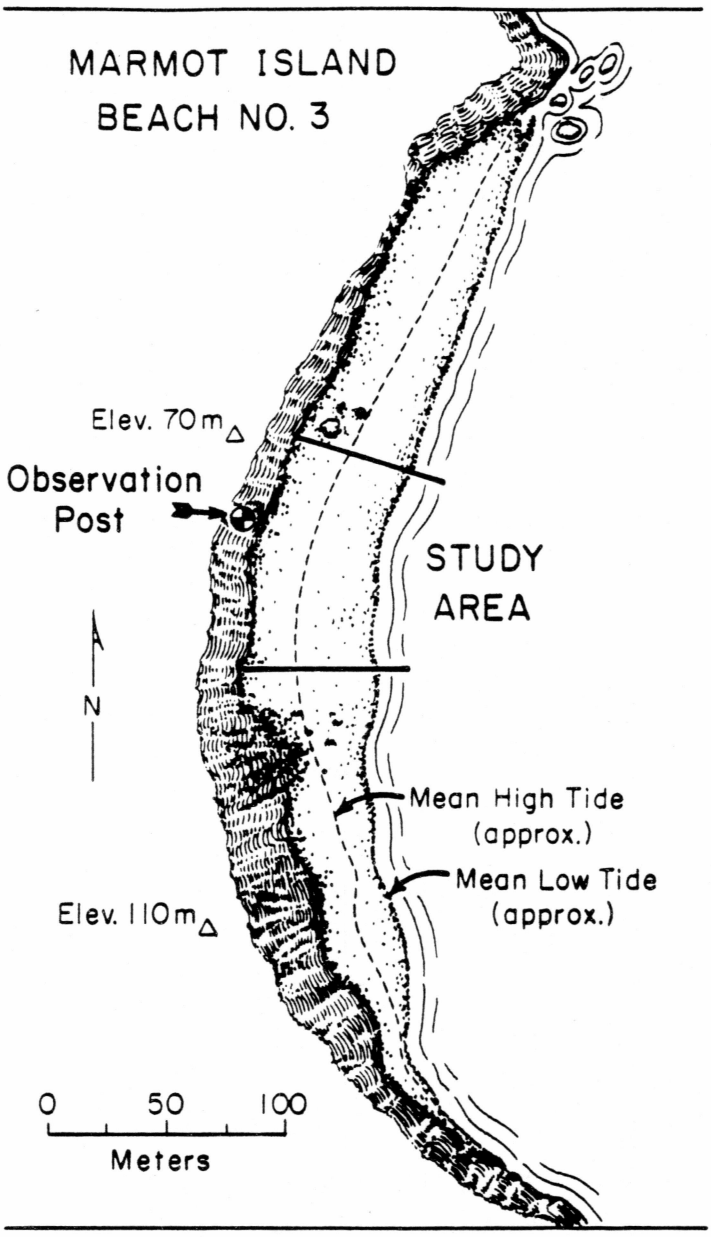

Figure 5. Map of beach 3 on Marmot Island showing study area used for the behavior study in 1981 (adapted from Aumiller, ADF&G unpubl. data)

Observations of sea lions were done with the aid of 10 X 40 binoculars and variable power (25 - 60) spotting scopes. Information was recorded directly into a field notebook or, in some instances, dictated into a tape recorder and later transcribed. All tide heights and times were obtained from Kodiak tide tables, using the correction for Ushagat Island for the Sugarloaf Island study area and the correction for Marmot Strait for the Marmot Island study area.

Population Counts

In the northern Gulf of Alaska, the breeding season of the Steller sea lion is thought to span a 2-month period from mid-May to mid-July (ADF&G unpubl. data). For the purposes of this study, the periods of time immediately before 15 May and immediately after 15 July will be referred to as the "prebreeding" and "postbreeding" seasons, respectively.

Counts of Steller sea lions were made on Sugarloaf Island from 15 April to 15 July 1978, 13 April to 10 July 1979, and 23 May to 10 August 1980. Total counts, sex and age composition counts and pupcounts were conducted daily in 1978 until mid-June and every second day thereafter. In 1979 and 1980 those counts were made twice weekly.

All counts on Sugarloaf Island were conducted from the slopes above the areas, usually without disturbing the animals. In 1978 and 1979, total counts were conducted only during the prebreeding and breeding seasons. In 1980 total counts were conducted during the breeding and postbreeding seasons. Since one complete count usually took from one to ten hours to conduct, the results are considered as estimates of the number of sea lions utilizing the study site, rather than as the actual number of sea lions present during any one day.

Total counts of sea lions were conducted on Marmot Island during the breeding season in 1979 by Alaska Department of Fish and Game personnel. For the purposes of this study, data collected from beaches 2 and 3 were the only data used in the analysis.

Prior to the onset of the breeding season (about 15 May), total counts of sea lions were the only types of counts conducted. During this prebreeding season period, the sea lions were in close-packed aggregations that made observations of each individual animal difficult. With the onset of pupping and breeding, the sea lions began to disperse and distribute themselves more evenly over the areas. This change in the distribution facilitated observation of individuals and allowed identification of their sex and age. Composition counts were conducted only after this change had taken place.

Sex and age composition counts were conducted on Sugarloaf Island during the breeding seasons of 1978, 1979 and 1980. The counts commenced on 15 May in 1978 and 1979 and on 23 May in 1980. Composition counts also were conducted on Marmot Island during the breeding season of 1979.

The age and sex of individual sea lions was determined by comparisons with known-aged animals and on the basis of secondary sexual characteristics. The following criteria were followed when classifying sea lions for composition counts.

Adult Female - Slender head and neck; presence of a nursing pup, yearling or juvenile; comparable in size to lactating females. (5+ years)

Adult Male - Much larger overall size than adult female; massive head, neck and shoulders. These males were classified further into:

Territorial Bull - Those adult males holding territories.

Non-Territorial Bull - Those adult males not holding territories.

Young Males - Head, neck and shoulders are developed enough to distinguish them from adult females but are much less developed than those of adult males.

Juveniles - Smaller than adult females and without the secondary sexual characteristics of males. Larger in size than yearlings and lacking the curly fur characteristic of many yearlings.

Yearlings - Born the previous year. Small overall size; many have slightly curly and darker fur than juveniles.

Pups - Young of the year.

No attempt was made to sex the juveniles, yearlings and pups, which were categorized only on the basis of size.

There is great individual variation in the size of sea lions in relation to age (Calkins and Pitcher 1982), hence the above categories, which were based mainly on size, are not necessarily accurate for age, except in the two youngest classes. In each year of the study, however, known-aged branded animals were present on the rookery, and I used these as my standards with which to compare and estimate the age of the other animals. I believe that this, along with behavioral observations, lent accuracy to the composition counts.

Branded Animals

The Alaska Department of Fish and Game branded sea lion pups at specific rookeries in the Gulf of Alaska in 1975 and 1976. Branding information is summarized in Table 1.

Observations of branded animals were made on Sugarloaf Island throughout the field seasons of 1978, 1979 and 1980, and on Marmot Island in 1979. For the purposes of this study only the age of the animal was recorded. Branded animals that were thought to be recognizable in the future were sketched in field notebooks. All brands that were seen more than once were noted and categorized as resights.

Behavior

Behavioral observations were conducted on Sugarloaf Island from 22 May to 10 August 1980 and on Marmot Island from 22 May to 10 July 1981. On Sugarloaf Island, observations were made from a blind on the slope above Area 5 (Fig. 3). On Marmot Island the blind was located approximately half way down the cliff behind Beach 3 (Fig. 5).

To assess the influence of the tides on the territorial behavior of Steller sea lions, a sampling program was designed around high and low tides. Behavioral observations were conducted for two hours before and two hours after high and low tides. Sea state and weather conditions

Table 1. Number of sea lion pups branded and the locations of branding in the Gulf of Alaska in 1975 and 1976 by Alaska Department of Fish and Game (Calkins and Pitcher 1982).

Location	Year	Number of pups branded
Sugarloaf Island, Barren Islands	1975	719
Marmot Island	1975	598
Total		1317
Sugarloaf Island, Barren Islands	1976	1443
Marmot Island	1976	3669
Outer Island, Kenai Peninsula	1976	249
Fish Island, P.W.S.	1976	29
Cape St. Elias, Kayak Island	1976	23
Seal Rock, P.W.S.	1976	316
Total		5729

also were recorded at the beginning and end of each sampling period.

All territorial bulls present on the study site at the beginning of each sampling period were identified and catalogued. Bulls were individually identified by noting the location of scars and fungal target lesions on their skin. Any changes in a bull's location and changes in numbers of bulls (newcomers or absentees) also were noted. No attempt was made to identify and monitor individuals other than territorial bulls, but the general location of cows and pups was noted throughout each sampling period.

All interactive behaviors of each bull were recorded on a continuous basis throughout each sampling period. The time of day, type and duration of each behavior and the location of the interaction on the study site were recorded. Interactive behaviors that were recorded are: territorial displays, chasing juveniles, fights, chasing adults, leaving territories and copulations.

I investigated two main aspects of territorial behavior at the Sugarloaf and Marmot Island rookeries; territorial displays and the chasing of juvenile animals. Territorial displays were composed of three types of stereotyped behaviors; three-way displays, mutual displays and boundary displays (Gentry 1970). Three-way displays took place along territory boundaries among three bulls; mutual displays were between two bulls. Boundary displays were displays along a territory boundary initiated by one bull toward another bull, with no response

from that bull. The three types of displays were grouped as territorial displays for analysis.

Chasing of juvenile animals took place when juvenile animals entered a bull's territory. The attending bull would chase the juvenile until the juvenile was out of the bull's territory. The entire episode, from the bull's first recognition of and movement toward the juvenile until the bull ceased chasing the juvenile was recorded as one chase. Territorial behaviors (chasing of juveniles and displays) were analyzed by comparing the number of behaviors per bull per hour in relation to tide height both within and between Sugarloaf Island and Marmot Island. In addition, in order to assess the importance of territory placement, territorial behavior was analyzed in relation to the position of a bull's territory within the Sugarloaf Island and Marmot Island rookeries.

Two other less frequently occurring territorial behaviors also were investigated: fights and the chasing of adult bulls. Fights between Steller sea lion bulls usually entail a dispute over territorial boundaries (Gisiner 1985; Gentry 1970). Fights may occur either between established bulls or between an intruding bull and an established bull (Gisiner 1985; Gentry 1970).

The chasing of adult bulls consisted of an established territorial bull chasing an intruding adult bull (either a territorial bull or nonterritorial bull) out of the established bull's territory. These chases usually were associated with a territorial bull leaving his territory for the water (or returning from the water).

All successful copulations that took place during the observation periods were recorded for each bull. Gentry (1970) and Gisiner (1985) have used the number of successful copulations as an indication of a bull's reproductive success based on the premise that Steller sea lion females usually only copulate once per season. I used the number of successful copulations that occurred at low and high tides to determine whether there was a difference between those tide stages in the overall copulation frequencies of the bulls, and I compared those results between the two islands. Copulation frequencies also were analyzed in relation to the placement of the territory on the rookery.

Territory size was estimated visually on both the Sugarloaf Island and Marmot Island study areas. Bad weather and rough seas prevented me from measuring the Sugarloaf Island territories at the end of the field season in 1980. In 1981, I was alone on Marmot Island during the last two weeks of the study and deemed that it was unsafe to attempt to clear the beach of sea lions without assistance.

Bulls were grouped by territory type and by island for statistical analysis of the behavior data. Kruskal-Wallis multiple comparisons tests were run to determine differences in behavior based on territory type. These multiple comparisons tests also were used to determine if the data could then be pooled by island for between island comparisons.

All statistical methods used follow Sokal and Rohlf (1979) and Conover (1981). Statistical packages used were from the Biomedical Computer Programs software (BMDP 1981). Kruskal-Wallis multiple comparisons were based on Conover (1980).

RESULTS

TOTAL COUNTS

Prebreeding Season Counts

Prebreeding counts on Sugarloaf Island commenced on 13 April in 1978 and on 22 April in 1979 and ended on 15 May in both years. In 1978 the average number of sea lions counted per day in that period was 664, with a high count of 1,324 on 28 April and a low count of 4 on 6 May. Eighteen of the 31 counts during this time were below the mean; 13 of the counts were above (Fig. 6A).

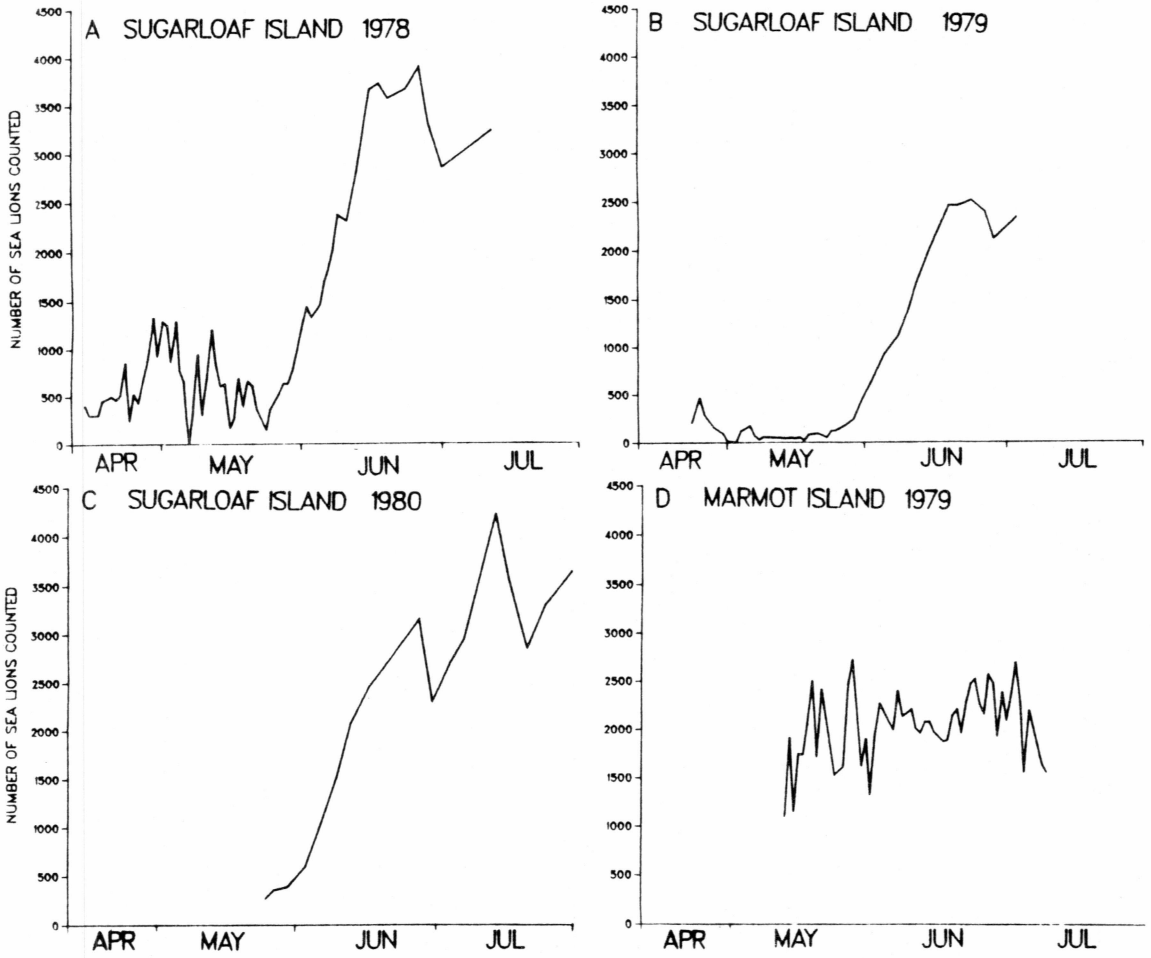

Figure 6. Total counts of sea lions conducted at the Sugarloaf Island rookery in 1978(A), 1979(B) and 1980(C), and at the Marmot Island rookery in 1979(D).

Corresponding counts made in 1979 ranged from a low of 7 on 1 May to a high of 463 on 24 April; the mean was 127. Eleven of the 15 counts made were below the mean; four were above (Fig. 6B).

Breeding Season Counts

Breeding season counts were conducted on Sugarloaf Island from 15 May to 12 July in 1978; 15 May to 3 July in 1979; and 23 May to 15 July in 1980 (Fig. 6A-C). In 1978 and 1979, the counts made early in the breeding season (15 May - 23 May) tended to follow the same patterns as did the counts conducted during the prebreeding seasons of the same years. In 1978, the numbers of sea lions present during the early part of the breeding season were variable, with high counts over 600 and a low count of 166. In 1979 the counts of sea lions for this same period remained low (under 100 individuals).

Counts conducted after 23 May in all years showed basically the same pattern, with numbers of sea lions increasing steadily until mid-June. After late June, the numbers of sea lions present on the study site became more variable, although the numbers remained much higher than in the prebreeding period.

The highest number of sea lions recorded on the study site during the breeding season in 1978 was 3,900 on 26 June. In 1979 the high count was 2,509 individuals on 23 June. A comparable peak of 3,159 animals was reached on 26 June 1980, followed by a comparable decrease

for several days, then a subsequent rise (Fig. 6C). The highest count in 1980 was 4,224 on 13 July.

Each year, the numbers of sea lions began to level off just prior to the high count in late June. In 1978, counts made from 15 June to 23 June were extremely close, ranging from a low of 3,573 on 19 June to a high of 3,725 on 17 June. In 1979, a "plateau" occurred between 18 and 20 June with 2,455 sea lions counted for each of these days. In 1980, however, the counts rose to a distinct peak.

Counts made after the late June peak in 1978, 1979 and 1980 were lower for several days before rising again in early July. In 1980, when the field season was a month longer, the number of sea lions counted rose to a second peak of more than 4,000 animals on 13 July, then decreased sharply until 20 July (2,854) before rising again in early August, at the end of the field season.

Counts of sea lions on beaches 2 and 3 of Marmot Island during the breeding season in 1979 were highly variable early in the breeding season (15 May-22 May), ranging from a low of 1,722 to a high of 2,500 (mean, 2,095) (Fig. 6D). Counts made after 22 May also tended to be variable (range, 1,330 - 2,720; mean, 2,076), least so between 1 June to 1 July (range, 1,460 - 2,580; mean, 2,143). There was no significant trend of increase comparable to the counts on Sugarloaf Island.

The largest number of sea lions counted on beaches 2 and 3 of Marmot Island in 1979 was 2,720 on 27 May. Another high count was 2,706 on 2 July. The lowest number of sea lions counted was 1,330 on 31 May. The average number of sea lions counted during the breeding season on the Marmot Island study site was 2,053. Fifteen of the 35 counts were above the mean and 20 were below.

Sex and Age Composition Counts

Five different categories were utilized when conducting composition counts on Sugarloaf Island: territorial bulls, adult cows, young bulls, juveniles and yearlings. The Marmot Island counts however were conducted using only four of the above categories (territorial bulls, adult cows, young bulls and juveniles), where the juvenile age class included yearlings as well as juveniles. For comparative purposes, therefore, yearlings and juveniles also have been combined into one age class (juveniles) for the Sugarloaf Island data.

The sex and age composition counts conducted during the early portion of the breeding season (15 May - 22 May) on Sugarloaf Island in 1978 showed variable numbers of all four age classes (Fig. 7A). Juveniles were the least numerous of the age classes in all counts conducted during this time. Cows, territorial bulls and young bulls, were the most numerous in one or more of these counts.

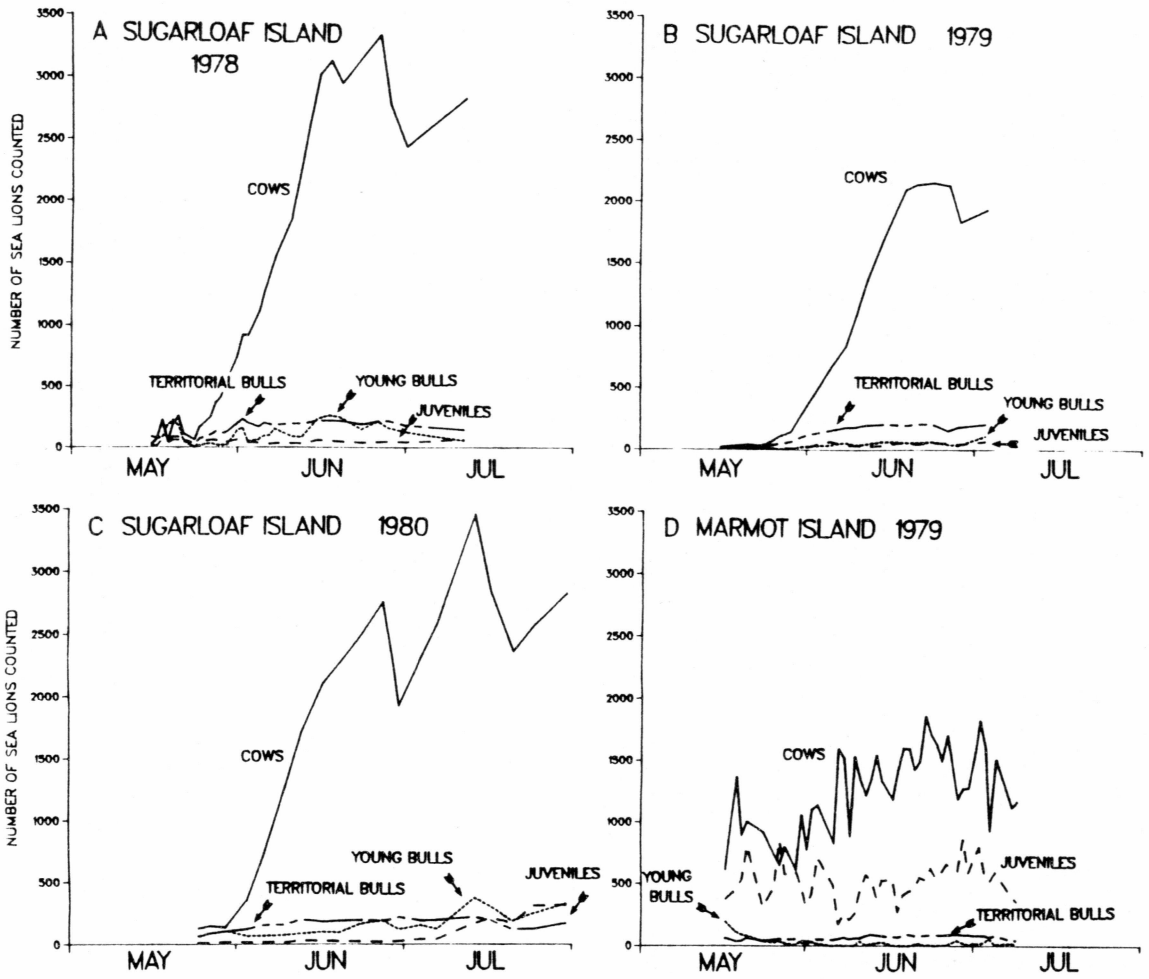

Figure 7. Sex and age composition counts of sea lions conducted at the Sugarloaf Island rookery in 1978(A), 1979(B), and 1980(C), and at the Marmot Island rookery in 1979(D).

In 1979, the sex and age composition counts on Sugarloaf Island were not as variable during the early part of the breeding season (15 May - 22 May) as they had been in 1978 (Fig. 7B). Total numbers also were lower than in 1978 for each of the sex and age categories except territorial bulls.

Composition counts conducted on Sugarloaf Island after the early part of the breeding season were all similar, in that the number of cows increased steadily from late May until reaching peak numbers in mid to late June (Fig. 7A,B,C). The numbers of territorial bulls, young bulls and juveniles, for the most part, remained about the same as they had been in the early part of the breeding season. Young bulls varied the most, from a low of zero to highs of over 250 animals.

Composition counts were conducted during the breeding and early postbreeding seasons on Sugarloaf Island in 1980 (Fig. 7C). The number of cows reached a peak in late June, as in the other years, and a seasonal high on 13 July, with lower numbers thereafter. This same trend can be seen in the numbers of young bulls and territorial bulls present in late July. The number of juveniles started to increase in early July, reaching their maximum on the last day that composition counts were made (30 July).

The results of the composition counts for Marmot Island in 1979 contrast markedly with those from the Sugarloaf Island counts in being much more variable and very different in overall composititon. The counts conducted during the early part of the breeding season showed both cows and juveniles present in variable numbers but consistently more numerous than either young bulls or territorial bulls (Fig. 7D).

The numbers of cows and juveniles continued to vary during the breeding season as they had earlier. Juveniles exceeded the number of cows in one count early in the breeding season (26 May), but they remained at a consistently lower level throughout the season, while the number of cows increased. A slight downward trend in the numbers of cows was suggested after a late June maximum in both the cow and the juvenile counts. Territorial bulls and young bulls remained at low levels with little variation throughout the breeding season.

The trends in the different sex and age classes throughout the breeding seasons on Sugarloaf Island are accentuated when the data for each class are expressed as proportions of the total numbers of sea lions present (Fig. 8A,B,C). Wide variation in the proportional composition can be seen early in the breeding season in both 1978 and 1979. The proportion of adult cows present early in the season ranged from 12 to 52 percent and 11 to 33 percent, respectively, of the total numbers present during this time. Territorial bulls comprised 13 to 32 percent of the total population early in the 1978 breeding season and 33

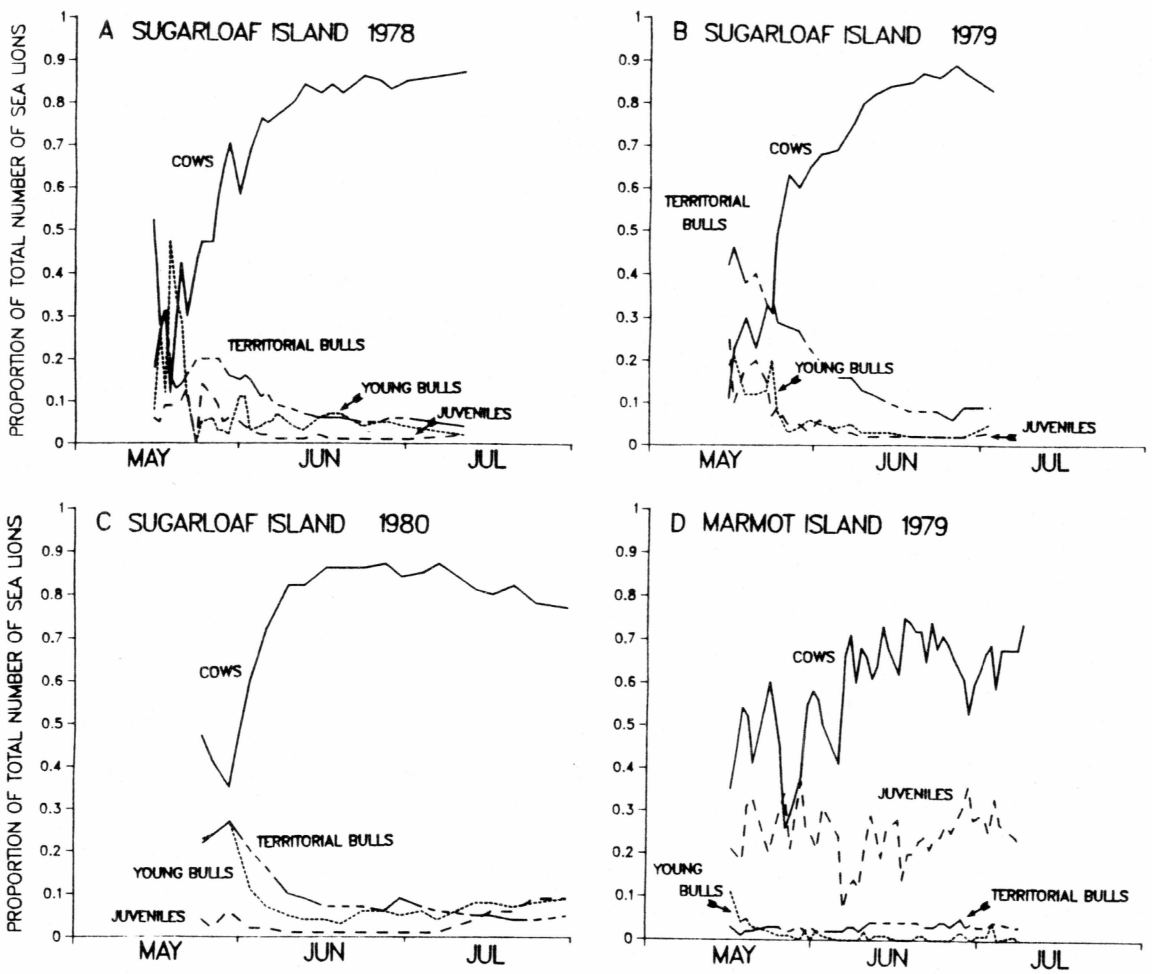

Figure 8. Sex and age composition counts of sea lions expressed as proportions of the total population on the Sugarloaf Island rookery in 1978(A), 1979(B) and 1980(C), and on the Marmot Island rookery in 1979(D).

to 46 percent early in 1979. Young bulls were 0 to 47 percent in 1978 and 12 to 20 percent in 1979. Juveniles ranged from 0 to 13 percent and from 6 to 25 percent, respectively, and were consistently in the lowest proportions during early part of the breeding season. In 1979 adult bulls comprised the highest proportion of animals present for all counts during the early part of the breeding season. Young bulls and juveniles were present in the lowest proportions, with adult cows present in intermediate proportions.

As the breeding season progressed each year on Sugarloaf Island, adult cows increased in proportion, making up 60 to 70 percent of the total population by 1 June and 80 to 90 percent by 10 June. The proportion of adult cows remained at this high level throughout the remainder of each breeding season, falling slightly in late July of 1980.

Territorial bulls, young bulls and juveniles decreased in relative numbers throughout the breeding season on Sugarloaf Island in all three years of the study. Young bulls were more variable throughout the breeding season in 1978 than they were in either 1979 or 1980, ranging from 0 to 11 percent of the total count. Juveniles were the most poorly represented class on Sugarloaf Island during the breeding season in all three years of the study, declining from May highs of up to 53 percent to lows of less than 1 percent in late June and early July. In mid-July of 1980, the proportion of juveniles began to rise again and reached a

maximum of 9 percent for the last two counts of the season.

The sex and age structure of the sea lions on Marmot Island contrasted markedly with that of the animals on Sugarloaf Island (Fig. 8D). The proportion of cows to the total count was extremely variable throughout the breeding season, ranging from a low of 26 percent to a high of 75 percent. The variation in the proportions decreased somewhat as the proportion of cows increased in June.

The proportion of juveniles present on the Marmot Island study site in 1979 also was extremely variable, ranging from a low of 7 percent to a high of 46 percent. Juveniles were present on the study site in consistently higher proportions than either territorial bulls or young bulls, throughout the breeding season. Territorial bulls remained in very low proportions, not exceeding 4 percent of the total animals present. Young bulls also were present on the Marmot Island rookery in very low proportions, usually not exceeding 2 percent of the total.

BRANDED ANIMALS

A total of 251 different branded animals were seen on Sugarloaf Island during the study period in 1978. Of these, 151 (61%) were two-year-olds and 100 (39%) were three-year-olds. In 1979, a total of 54 different branded animals were seen, 29 (54%) of which were three-year-olds, and 25 (46%) were four-year-olds. Five hundred

sixty-five different branded animals were seen during the study in 1980. Of these, 306 (54%) were four-year-olds, and 259 (46%) were five-year-olds.

In 1978, daily numbers of branded animals sighted were variable for both two- and three-year-olds, especially prior to the end of May (Fig. 9A). Daily counts of branded three-year-olds were low during May and June and increased slightly in July. Two-year-olds were seen in low numbers throughout May, June and July. The highest count of branded two-year-olds was 27 on 3 May. The highest count of three-year-olds was 8 on 27 and 28 April. Counts of two- and three-year-olds were significantly correlated ($r=.4387$; $p=.01$) during the pre-breeding season of 1978.

In 1979 daily numbers of branded animals sighted were low throughout the study but tended to be lowest in the middle of the breeding season and highest in the early and late breeding periods (Fig. 9B). The highest number of three-year-olds seen in 1979 was four on 7 July. The highest number of four-year-olds was four on 29 April and on 6 and 7 July.

In 1980, the daily numbers of branded four-year-olds sighted were variable but low (< 10/day) until 12 July, when 19 were seen (Fig. 9C). From 12 July until the end of the study in August, daily sighting of branded animals were consistently higher than on any date prior to 12 July. An increasing trend in the daily numbers of branded

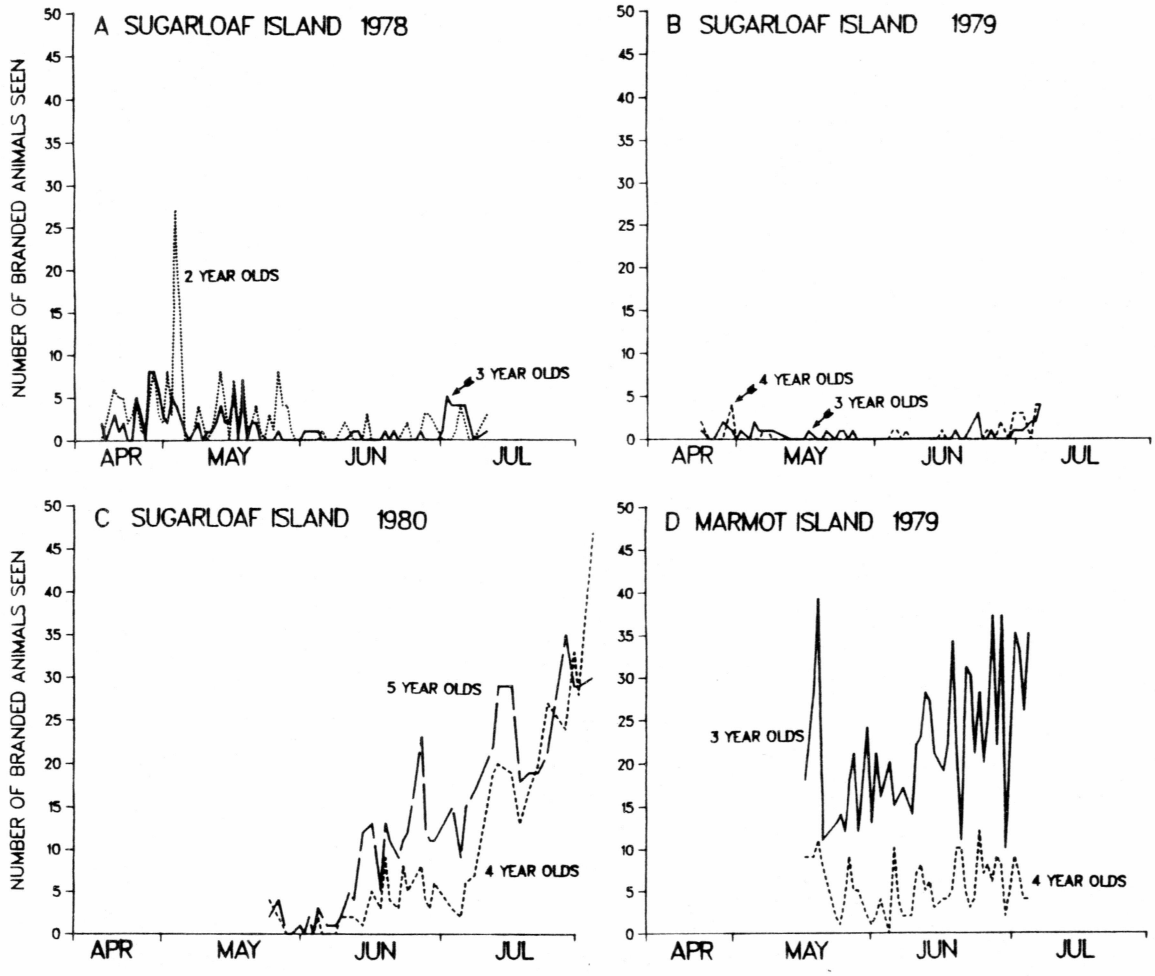

Figure 9. Observations of branded animals on the Sugarloaf Island rookery in 1978(A), 1979(B) and 1980(C), and on the Marmot Island rookery in 1979(D). Branded animals were 2 and 3 years old in 1978, 3 and 4 years old in 1979, and 4 and 5 years old in 1980.

four-year-olds can also be seen during this time. The highest count of branded four-year-olds was 47 on 4 August.

Daily sightings of branded five-year-olds also were low initially (< 5 animals/day) until 13 June, when 12 were sighted. After this date, the numbers were variable but generally increased throughout the remainder of the study. The high count of branded five-year-olds was 35 on 28 July.

In 1980, branded cows were seen with pups for the first time. All of these cows (7) were 5 years old. No known aged cows were seen with pups prior to the 1980 field season.

On Marmot Island in 1979, a total of 1,306 sightings of branded animals were recorded. Of these, 1,041 (80%) were of three-year-olds and 265 (20%) were of four-year-olds. The number of sightings per day was comparatively high but extremely variable (Fig. 9D). The highest daily count of branded three-year-olds was 39 on 19 May. The highest count of four-year-olds was 12 on 24 June. No estimate was made to determine the actual number of different animals that these sightings represented.

Counts of branded three-year-olds on Marmot Island in 1979 were highly correlated with the total number of cows present on the rookery ($r = .4207$; $p = .01$). This was not true for counts of four-year-olds at any level. Counts of branded three-year-olds were not positively or

negatively correlated with counts of branded four-year-olds.

BEHAVIOR

The behavior of bulls was analyzed within islands by territory type and between islands by pooling territory types. Kruskal-Wallis multiple comparisons tests (Conover 1980) were run to determine if interaction effects were unimportant between territory types within Sugarloaf and Marmot Islands, thereby allowing the data to be pooled by island.

In all behaviors tested the Sugarloaf Island bulls occupying landlocked and water-access territories did not differ significantly from one another. The Sugarloaf Island bulls however, did differ significantly from the bulls occupying each of the territory types on Marmot Island (landlocked, tidal and semiaquatic). The Marmot Island bulls differed from one another for certain behaviors and at certain tide stages, but these differences were not consistant for all behaviors and tide stages.

I feel these interaction effects between bulls on Marmot Island are due to the influence of the tide and are unimportant in the overall comparisons of the two islands (Neter and Wasserman 1974). Therefore, the data for Marmot Island also were pooled for overall comparisons with Sugarloaf Island in the following analysis. The behaviors of bulls in different territory types were investigated only within the two islands.

Types of Territories

Bulls occupied two types of territories on the Sugarloaf Island study area in 1980. I defined "landlocked territories" as those in which the bulls had no access to water along any edge of their territory. "Water-access territories" were those where the bulls had access to the water along at least one edge of their territory. Both landlocked and water-access territories were above the high tide. Four territories were classified as being landlocked and six as having access to water during the 1980 field season (Fig. 10).

All boundaries between territories on Sugarloaf were distinguished by topographic features of the study area. A rift 1 to 2 meters in width separated the territories of Bulls 1, 1A and 6 from the territories of Bulls 4, 4A and 7 (Fig. 10). The remaining territory boundaries were established along small cracks and uplifted segments of rock.

The territories occupied by bulls on the Marmot Island study area in 1981 were of three types: "landlocked", "tidal" and "semi-aquatic" (Figs. 11-12). Landlocked territories were those in which the bulls had access to the water only at high tide stages. Tidal territories were those within the littoral zone, where the bulls had access to the water and unwashed sections of the beach at all tide stages. Semi-aquatic territories were at or near the low tide line, and the bulls in them were almost constantly in the water. These bulls had access to the

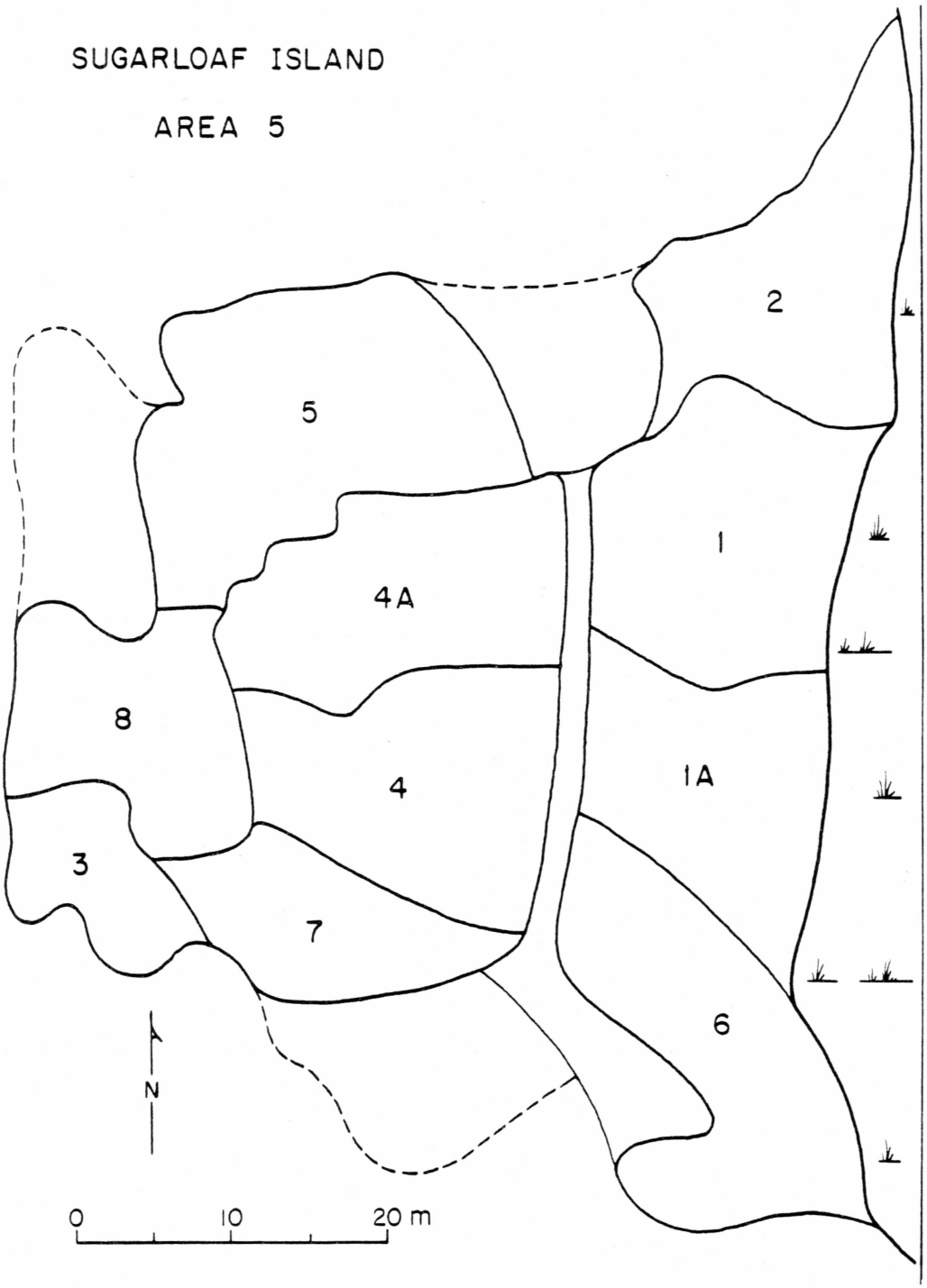

Figure 10. Area 5 of Sugarloaf Island showing territories of bulls in 1980. Bulls 1, 1A, 4 and 4A held landlocked territories. Bulls 2, 3, 5, 6, 7 and 8 held water territories. Dashed lines denote low areas.

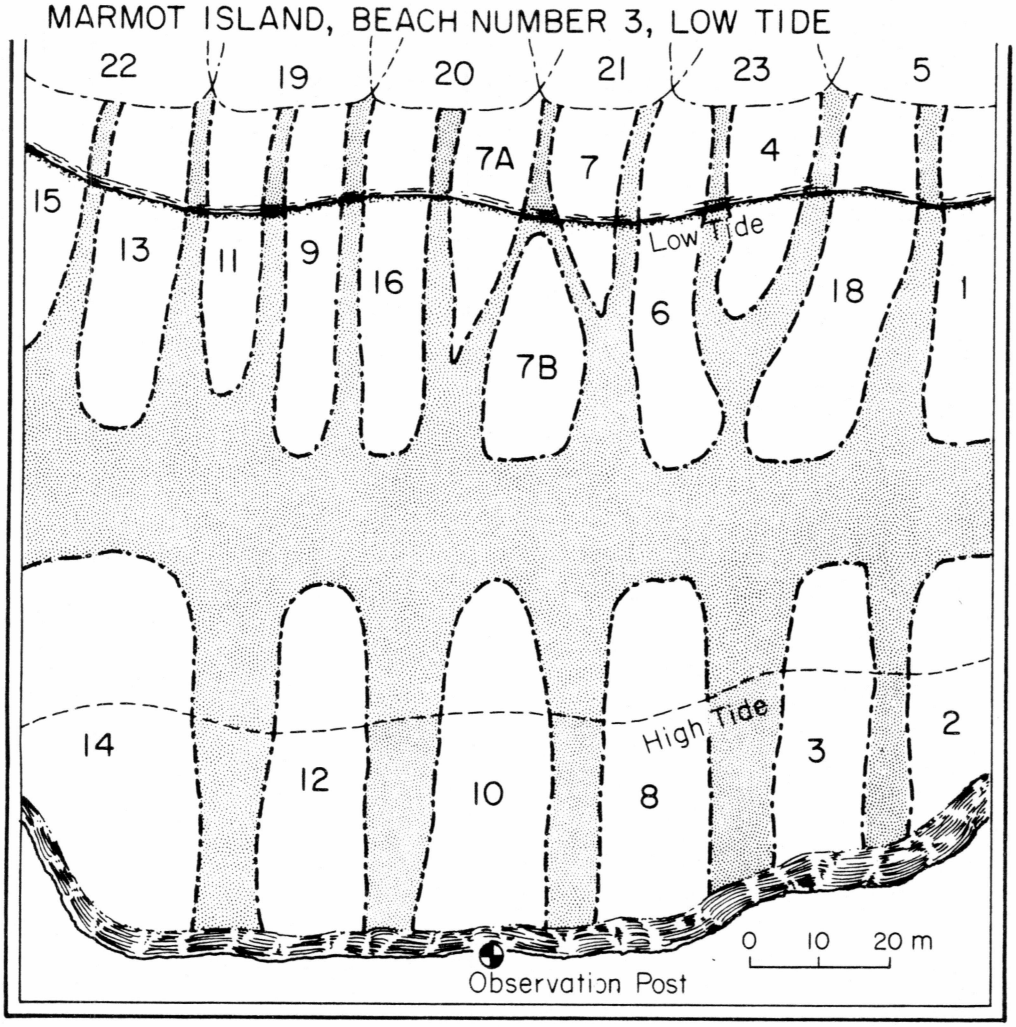

Figure 11. Study area of Beach 3 on Marmot Island showing the distribution of territories at low tide in 1981. Bulls 1, 4, 6, 7, 7A, 7B, 9, 11, 13, 15, 16 and 18 held tidal territories. Bulls 2, 3, 8, 10, 12, 14 held landlocked territories. Bulls 5, 19, 20, 21, 22 and 23 held subaquatic territories. Shaded portions denote areas of overlap between territories.

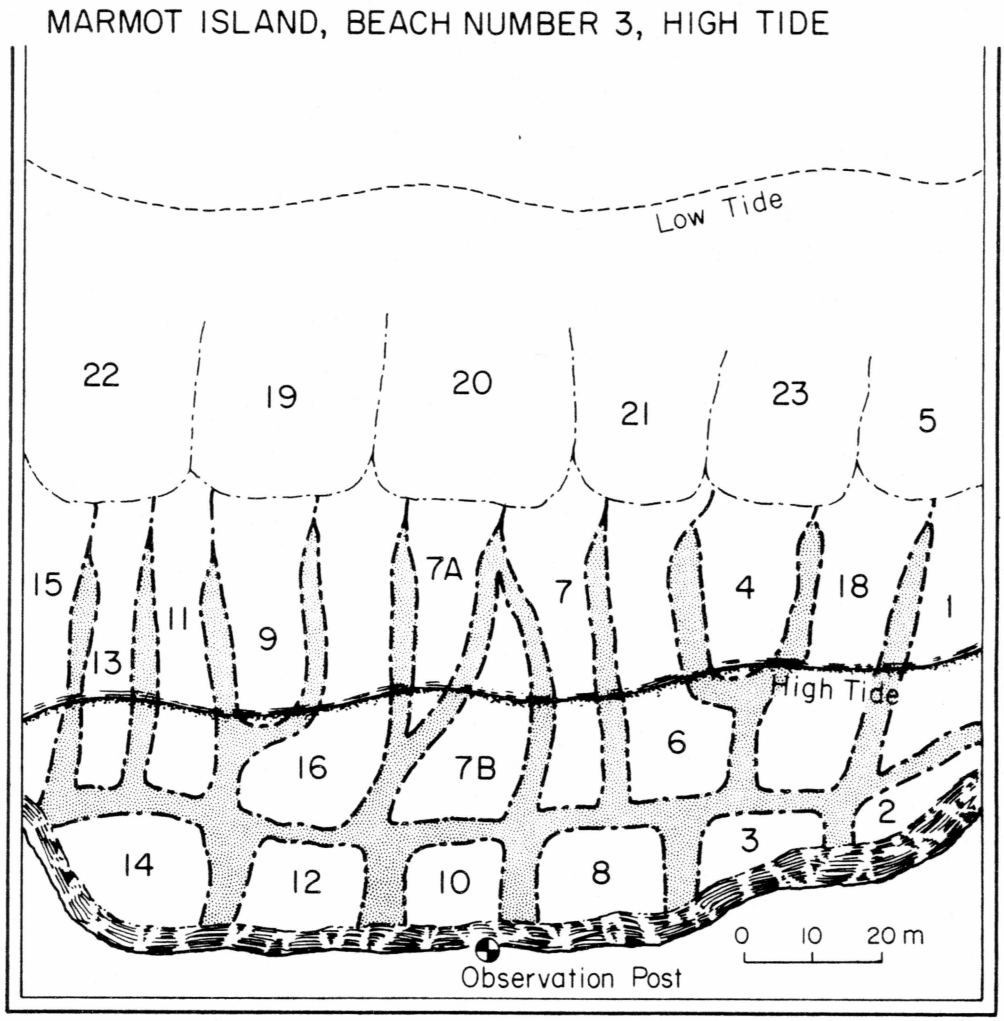

Figure 12. Study area of Beach 3 on Marmot Island showing the distribution of territories at high tide in 1981. Bulls 1, 4, 6, 7, 7A, 7B, 9, 11, 13, 15, 16 and 18 held tidal territories. Bulls 2, 3, 8, 10, 12, 14 held landlocked territories. Bulls 5, 19, 20, 21, 22 and 23 held subaquatic territories. Shaded portions denote areas of overlap between territories.

beach only at lower tide stages. Six territories were classified as landlocked, 12 were classified as tidal and 6 as semi-aquatic during the 1981 field season (Figs. 11-12).

Number of Territories and Duration of Occupancy

Ten bulls held territories on Area 5 of Sugarloaf Island during the breeding season in 1980. The first territorial bull on the study area was recorded on 22 May. Eight of the 10 bulls were present on their territories by 26 May (Table 2). The remaining two bulls were present by 8 June. The mean duration of a bull's tenure on the Sugarloaf Island study area was 44 days (range, 34 - 52 days; n=10 bulls). The first departure date was 26 June. Forty percent (4) of the original 10 bulls had left their territories by the end of the first week of July. All of the 10 bulls had left their territories by 17 July.

Thirty-nine bulls occupied territories on the Marmot Island study area during the breeding season in 1981. The first bulls to occupy territories on the Marmot Island study area arrived on 25 May. Sixty-five percent (15) of the 24 bulls were present by 31 May (Table 3). The remaining 8 were present by 7 June. The mean duration for bulls on the Marmot Island study area was 22 days (range, 2 - 40 days; n=29). The first bulls departed on June 13. All of the original 24 bulls had left their territories by the end of the first week of July.

Table 2. Territory types, arrival and departure dates, and durations for territorial bulls on the Sugarloaf Island study area in 1980.

Bull number	Territory type	Arrival date	Departure date	Duration (days)
5-1	Landlocked	22 May	30 June	40
5-2	Water-access	23 May	26 June	34
5-3	Water-access	23 May	12 June	50
5-4	Landlocked	24 May	8 July	45
5-5	Water-access	24 May	29 June	37
5-6	Water-access	25 May	13 July	49
5-7	Water-access	26 May	17 July	52
5-8	Water-access	26 May	13 July	48
5-1A	Landlocked	6 June	20 July	42
5-4A	Landlocked	8 June	18 July	41

Table 3. Territory types, arrival and departure dates, and durations for territorial bulls on the Marmot Island study area in 1981.

Bull number	Territory type	Arrival date	Departure date	Duration (days)
1	Tidal	25 May	30 June	36
2	Landlocked	25 May	21 June	27
3	Landlocked	25 May	22 June	28
4	Tidal	25 May	4 July	40
5	Semiaquatic	25 May	24 June	30
6	Tidal	26 May	25 June	31
7	Tidal	26 May	3 July	38
8	Landlocked	26 May	3 July	37
9	Tidal	26 May	28 June	32
10	Landlocked	27 May	3 July	37
11	Tidal	27 May	29 June	32
12	Landlocked	27 May	25 June	29
13	Tidal	28 May	13 June	15
14	Landlocked	30 May	25 June	25
15	Tidal	30 May	22 June	22
16	Tidal	3 June	19 June	16
18	Tidal	3 June	30 June	27
7A	Tidal	3 June	13 June	10
7B	Tidal	3 June	30 June	27
19	Semiaquatic	5 June	19 June	14
20	Semiaquatic	6 June	19 June	13
21	Semiaquatic	6 June	20 June	14
22	Semiaquatic	6 June	5 July	29
23	Semiaquatic	12 June	29 June	17

The durations of breeding season territorial bulls holding different types of territories on the Sugarloaf Island and Marmot Island study areas were compared using Kruskal-Wallis multiple comparisons tests (Conover 1980). No difference was found between the durations of bulls holding landlocked and water-access territories on the Sugarloaf Island study area. There also was no difference found in duration between the bulls holding landlocked, tidal and semiaquatic territories on the Marmot Island study area.

The data were pooled for Sugarloaf Island and Marmot Island and compared using a Mann-Whitney test for differences in means. The Sugarloaf Island bulls had significantly longer durations on their territories than did the Marmot Island bulls (Mann Whitney: $U=8.50$; $n_1=24$, $n_2=10$; $p=0.000$).

Territorial Behavior

I observed thirty-nine chases of juveniles on the Sugarloaf Island study area in 1980. An average of 0.50 chases per hour occurred at low tide and 0.46 chases per hour at high tide (Fig. 13). The numbers of chases per hour at low and high tides were compared using the Mann-Whitney test for differences between means. No statistical difference was found in the number of chases per hour between high and low tides (Mann-Whitney: $U=25.50$; $n_1=8$, $n_2=6$; $p=.8435$).

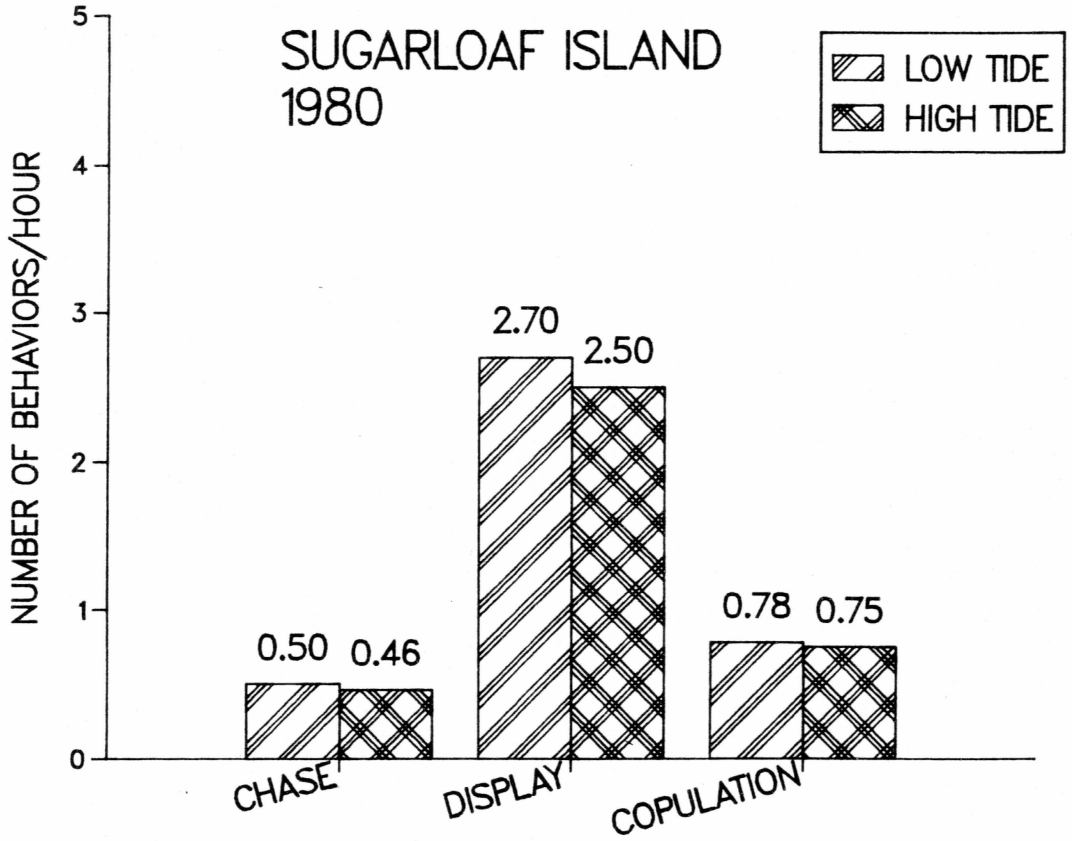

Figure 13. Comparisons between tides of the frequency of juvenile chases, territorial displays and copulations by territorial bulls on the Sugarloaf Island study area in 1980.

For all tide stages combined, 199 territorial displays were observed on Sugarloaf Island during the 1980 field season. An average of 2.7 displays per hour occurred at low tide and 2.5 per hour at high tide (Fig. 13). The difference between these means was not significant (Mann-Whitney: $U=27.00$; $n_1=8$, $n_2=6$; $p=.6979$).

To assess the influence of territory type on the territorial behavior of bulls on Sugarloaf Island, the number of chases of juveniles per hour and the number of displays per hour were compared for bulls holding landlocked territories versus bulls holding water territories. The results of these comparisons at low and high tides are compiled in Table 4. No significant difference was found in any of the comparisons.

I observed 1,020 chases of juveniles on the Marmot Island study area in 1981. An average of 16.2 chases per hour occurred at low tide and 5.0 chases per hour at high tide (Fig. 14). The difference was highly significant (Mann-Whitney: $U=95.00$; $n_1=8$, $n_2=13$; $p=.0018$).

One thousand two hundred thirty-four boundary displays were observed in all sampling periods on Marmot Island in 1981. The average number of displays per hour during the low tide sampling periods was 6.86. The high tide average was 14.07 displays per hour (Fig. 14). This difference is highly significant (Mann-Whitney: $U=21.00$; $n_1=8$, $n_2=13$; $p=.0247$).

Table 4. Results of Mann-Whitney tests comparing the frequency of juvenile chases, displays and copulations for landlocked and water bulls on the Sugarloaf Island rookery in 1980.

Tide level	Behavior	Bull type[1]	Significance[2]	Mann-Whitney test statistic[3]
Low	Juvenile Chase	LL vs W	ns	U=03.00; p=0.0746
	Display	LL vs W	ns	U=15.50; p=0.1761
	Copulation	LL vs W	ns	U=15.00; p=0.2148
High	Juvenile Chase	LL vs W	ns	U=10.50; p=0.7347
	Display	LL vs W	ns	U=18.50; p=0.1593
	Copulation	LL vs W	ns	U=16.50; p=0.3269

1 LL=landlocked; W=water
2 ns=not significant
3 $n_1=4$; $n_2=6$

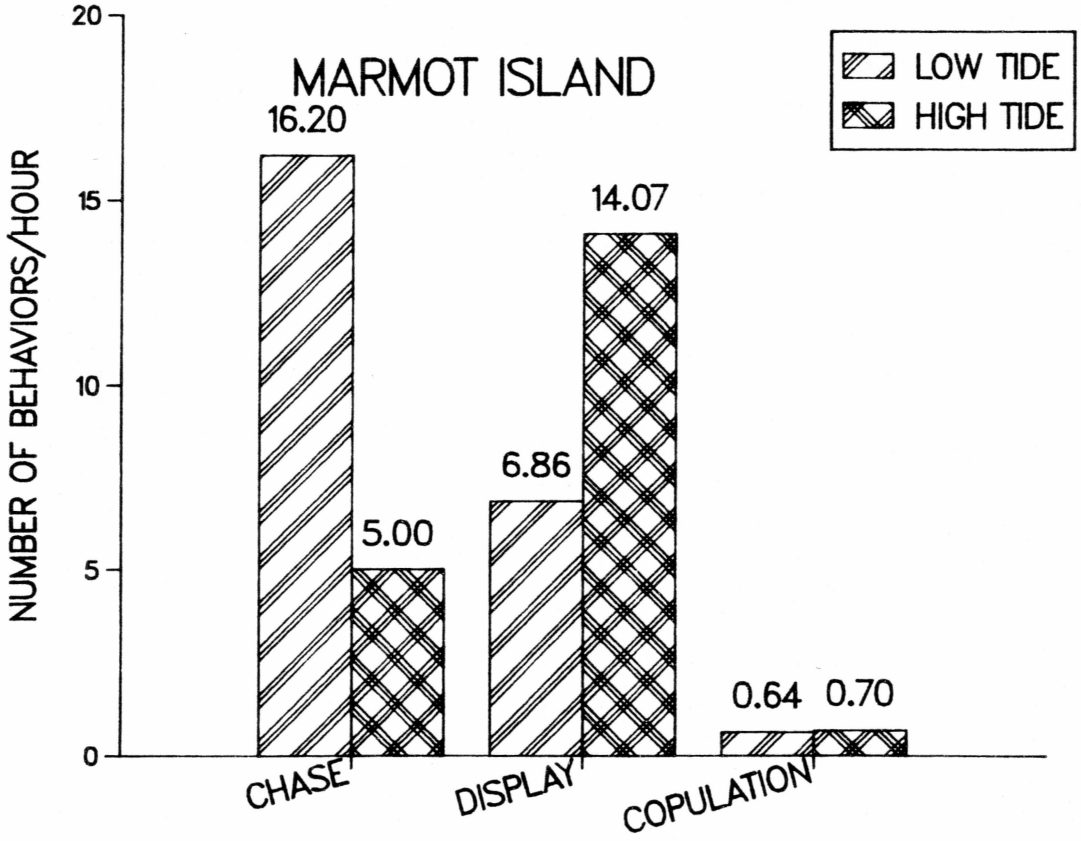

Figure 14. Comparisons between tides of the frequency of juvenile chases, territorial displays and copulations by territorial bulls on the Marmot Island study area in 1981.

The relationship between territory type and the territorial behavior of bulls on Marmot Island also was investigated by comparing the number of chases per bull per hour and the number of displays per bull per hour for landlocked, tidal and semiaquatic bulls (Table 5). Significant differences were found in two of the four comparisons. The frequency of juvenile chases among territory types was significant at high tide, as was the frequency of displays. In each of the significant cases, a Kruskal-Wallis multiple comparisons test (Conover 1980) was used to determine between which pairs of territory types the significance lay (Table 6).

The territorial behavior of Sugarloaf Island bulls was compared with that of Marmot Island bulls in terms of the frequency of chases and displays per bull per hour for low tide and high tide observation periods (Fig. 15). The number of chases per bull per hour was significantly greater on the Marmot Island study area than on the Sugarloaf Island study area during both the low and the high tide observation periods, (Mann-Whitney: (low tide) $U=0.00$; $n_1=8$, $n_2=8$; $p=.0007$; (high tide) $U=11.50$; $n_1=6$, $n_2=13$; $p=.0156$). There was no significant difference between islands in the frequency of displays per bull per hour for low tide (Mann-Whitney: $U=30.00$; $n=8$, $n=8$; $p=.8333$), but the difference at high tide was significant (Mann-Whitney: $U=12.00$, $n_1=6$, $n_2=13$; $p=.0177$).

Table 5. Results of Kruskal-Wallis tests comparing the frequency of juvenile chases, displays and copulations for landlocked, tidal and semiaquatic bulls on the Marmot Island rookery in 1981.

Tide level	Behavior	Bull type LL vs T vs SAQ [1]	Kruskal-Wallis test statistic [3]
Low	Juvenile Chase	ns [2]	U=03.51; p=0.1733
	Display	ns	U=03.86; p=0.1450
	Copulation	S	U=07.36; p=0.0283
High	Juvenile Chase	S	U=06.93; p=0.0312
	Display	S	U=06.37; p=0.0416
	Copulation	S	U=10.34; p=0.0065

1 LL=landlocked; T=tidal; SAQ=semiaquatic
2 ns=not significant; S=significant
3 $n_1=6$; $n_2=12$; $n=6$

Table 6. Results of Kruskal-Wallis multiple comparisons tests comparing the frequency of juvenile chases, displays and copulations between landlocked, tidal and semiaquatic bulls on the Marmot Island study area in 1981.

Tide	Behavior	Kruskal-Wallis test statistic[1]		
		LL vs T[2]	LL vs SAQ	T vs SAQ
Low	Juvenile Chase	ns[3]	ns	ns
	Display	ns	ns	ns
	Copulation	S (T=8.568)	ns	S (T=8.010)
High	Juvenile Chase	ns	S (T=10.112)	S (T=12.107)
	Display	S (T=10.571)	ns	S (T=9.582)
	Copulation	ns	S (T=9.871)	S (T=12.857)

1 p .05; $n_1=6$; $n_2=12$; $n_3=6$
2 LL=landlocked; T=tidal; SAQ=semiaquatic
3 ns=not significant; S=significant

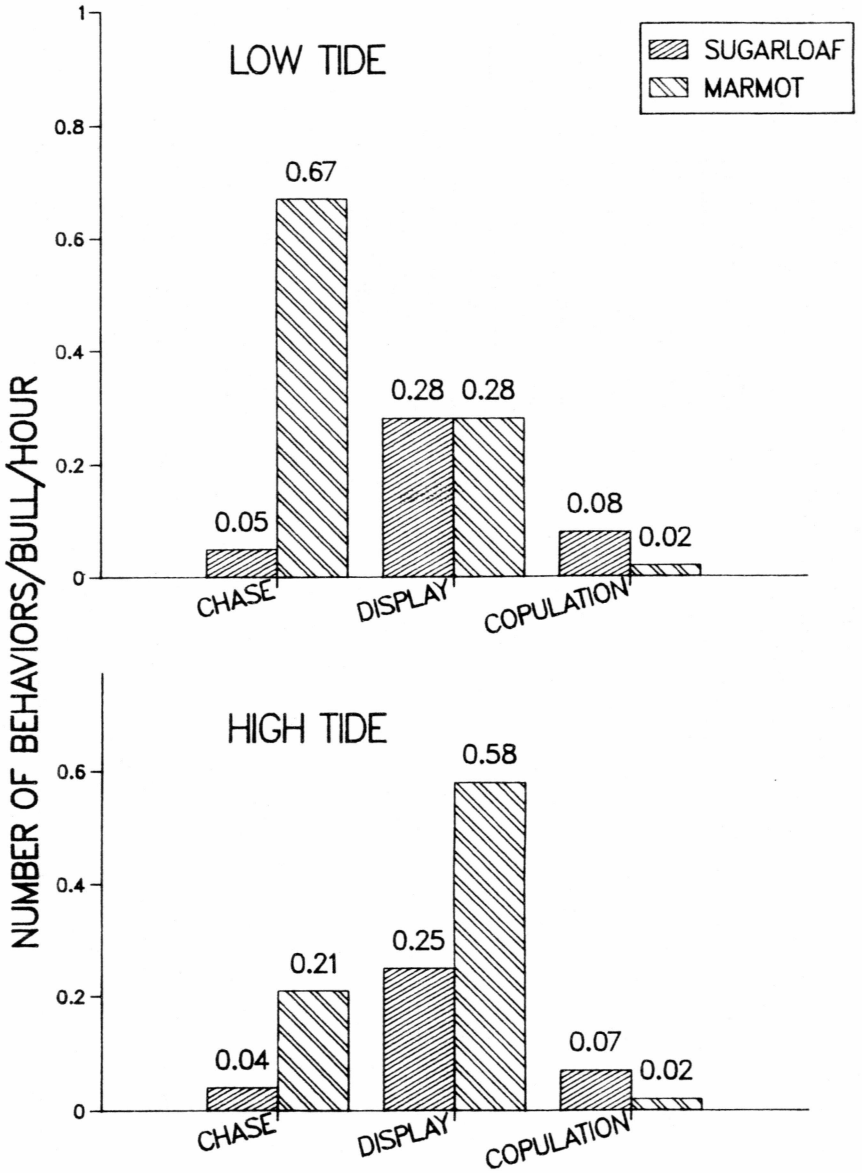

Figure 15. Comparisons between islands of the frequency of juvenile chases, territorial displays and copulations by territorial bulls at low and high tides: Sugarloaf Island in 1980 and Marmot Island in 1981.

Reproductive Behavior

Fifty-nine successful copulations by territorial bulls were observed on the Sugarloaf Island study area in 1980. The average frequency of copulations at low tide was .78 per hour. At high tide, the average frequency was .75 copulations per hour (Fig. 13). The number of copulations at low tide observation periods was not significantly different from the number of copulations at high tide observation periods (Mann-Whitney: $U=24.50$; $n_1=8$, $n_2=6$; $p=.9473$).

The bulls' success in copulation in relation to the type of territory they held was examined by comparing the number of copulations per hour for bulls on landlocked versus water-access territories on the Sugarloaf Island study area (Table 4). There was no significant difference between them (Mann-Whitney: (low tide) $U=15.00$; $n_1=4$, $n_2=6$; $p=.2148$; (high tide) $U=16.50$; $n_1=4$, $n_2=6$; $p=.3269$).

Ninety-two successful copulations by bulls on the Marmot Island study area were observed in 1981. The average number of copulations per bull per hour at low tide was .64, and at high tide it was .70 (Fig. 14). The differences in numbers of copulations per bull per hour per high and low tide observation period were not significant (Mann-Whitney: $U=54.00$; $n_1=8$, $n_2=13$; $p=.8829$).

The success in copulation of bulls holding landlocked, tidal and semiaquatic territories on the Marmot Island study area were compared between high and low tides. The frequency of copulations was significant at both low and high tides (Table 5). Kruskal-Wallis multiple comparisons tests (Conover 1981) were run to determine the significance level between each of the pairs of territory types (Table 6).

The number of copulations per bull per hour was computed for each high tide and low tide observation period for both the Sugarloaf Island and the Marmot Island study areas by pooling the data by tide (Fig. 15). No significant difference was found in the number of copulations per bull per hour at the Sugarloaf Island study area versus the Marmot Island study area for low tides (Mann-Whitney: $U=43.00$; $n_1=8$, $n_2=8$; $p=.2434$) or high tides (Mann-Whitney: $U=51.00$; $n_1=6$, $n_2=13$; $p=.2848$).

Other Behaviors

Territorial bulls occasionally abandoned their territories for the water, presumably for thermoregulatory purposes. Territorial bulls were observed leaving their territories on six occasions on Sugarloaf Island. On two of these occasions, bulls left landlocked territories; the remaining four cases were of bulls leaving water-access territories. Thirty-seven instances of bulls leaving territories on Marmot Island

were recorded in 1981. Bulls left landlocked territories 14 times and tidal territories 23 times. Bulls on subaquatic territories did not leave for the water.

Chases of adult bulls occurred on the rookeries usually as a result of a territorial bull leaving or returning to his territory. Seven chases of adult bulls were observed on Sugarloaf Island; four of these were by bulls on water-access territories and three were by landlocked bulls. I observed 118 chases of adult bulls on the Marmot Island rookery in 1981. Landlocked bulls chased adult bulls 14 times, bulls on tidal territories chased adult bulls 104 times and bulls on subaquatic territories chased other bulls 57 times.

No fights were observed on the Sugarloaf Island rookery, however, the apparent results of 2 fights (new wounds on bulls, presence of fresh blood) were noted. Both of these presumed fights occurred as a result of new bulls arriving on the study area (bulls 1A and 4A), usurping portions of other bulls' territories (bulls 1 and 4). Two fights were observed on the Marmot Island rookery in 1981.

DISCUSSION

POPULATION

Sugarloaf Island

The use of Sugarloaf Island by Steller sea lions outside the breeding season has been documented by the Alaska Department of Fish and Game through aerial surveys flown in the mid to late 1970's. The numbers varied among these surveys but indicated generally that Sugarloaf Island is used as a haulout in "low" numbers in early spring and late fall. No data are available on the use of the island during the winter months.

The haulout behavior of Steller sea lions outside the breeding season has not been well-studied or documented. Most of the available information is based on observations made during the breeding season and usually only on that segment of the population involved in breeding activities.

Prebreeding season counts of sea lions conducted on Sugarloaf Island during 1978 revealed hourly and daily variations in the numbers of sea lions utilizing the island as a hauling area. The daily variation in the numbers of sea lions hauling out may be a reflection of the within-day variation, as well as the turnover of individuals utilizing the island during the prebreeding season. Resightings of

recognizable individuals on Sugarloaf Island during the nonbreeding season indicated that many were present on the island only for a few days. Also, recognizable groups of sea lions (young males) occasionally would appear on the island, occupy a specific location, and then leave within a few days, indicating that Sugarloaf Island was used by them only as a temporary haulout, and that it may be used more as a resting area for animals moving through the Gulf at this time of year than as a permanent base. This same pattern of transient use has been noted for sea lions hauling out at Cape St. Elias in the eastern Gulf of Alaska (ADF&G unpubl. data).

The population on Sugarloaf Island during the prebreeding season was composed of both sexes and most age classes. Although complete sex and age composition counts were not taken during this prebreeding period, animals in each sex/age class were noted, except for adult bulls and pups. Bulls did not begin to arrive until early to mid May, and most pups were not born until late May. The sightings of branded animals on the island during each prebreeding season were evidence of the age of juveniles present on the island during this time of the year.

The variation seen in the early breeding season counts on Sugarloaf Island is attributable in part to the transition in its use from haulout to rookery. On the portion of the island not used by sea lions during

the prebreeding season, the first animals to arrive were territorial bulls. As May progressed, more and more bulls arrived, followed closely by cows and attending juveniles. This progression also takes place on the portion of the island used as a spring haulout area, but the change is not as evident, because of the continuing presence of juveniles. As territorial bulls and cows arrive, the nonbreeding segment of the population eventually leaves the rookery. This change from haulout to rookery and the subsequent dispersal of the nonbreeding subadults also has been described by Gentry (1970) from his observations of the sea lions at the Ano Nuevo rookery in California.

The onset of the breeding season for Steller sea lions in the Gulf of Alaska has been set at mid-May by ADF&G (Calkins and Pitcher 1979) and is based upon the births of the first surviving pups. The changeover from hauling area to rookery on Sugarloaf Island, however, actually took place during the first 3 weeks in May. The first territorial bulls were noted arriving on the island in early to mid-May in both 1978 and 1979, and their numbers increased steadily throughout this 3-week period. Pregnant cows began to arrive on these same areas approximately 1 week later than the first arriving bulls and continued to arrive until mid-June. The juvenile animals noted during the prebreeding season remained on these areas until approximately the end of May. By June, most of these juveniles were absent from the rookery.

All of May is, therefore, a period of transition on Sugarloaf Island with previously unused areas changing to breeding areas by the first week of May, while other areas still are occupied by juveniles until the end of May. By early June, the island has become a rookery, with nearly all areas used for breeding and pupping.

Once the changeover from haulout to rookery was completed, the population began to increase rapidly. Most of this increase was due to the arrival of pregnant cows. The number of territorial bulls in June remained constant and was virtually the same in all years. Young bulls and juveniles, however, were in variable but low numbers, reflecting the transient nature of this segment of the population.

The increase in the total numbers reached a peak during the third week of June in all three years. During the time of this peak, the proportion of cows was somewhat variable but ranged between 80 and 90 percent of the total non-pup population. This peak was somewhat rounded in 1978 and 1979 but more distinct in 1980, possibly because of less frequent counts made during that year. Nevertheless, the proportion of the cows to the total population in 1980 was similar to that of 1978 and 1979.

Yearly variation in the numbers of sea lions present on Sugarloaf Island at the time of the peak counts in June was marked. The 1979 maximum was about 1400 animals lower than in 1978, rising again by 650 animals in 1980. Such variation might be due to a shift in their food

resources, weather conditions and/or the general movement patterns of sea lions throughout the Gulf. Yearly variation of that magnitude is unusual. Although wide variation in numbers between years has been noted at other hauling areas in the Gulf (Mathisen and Lopp 1963; Calkins and Pitcher 1979), the numbers have been from spot counts from aircraft, rather than long-term daily counts.

Immediately after the late June high counts in all three years, the total number of cows dropped off sharply, reaching a low count in the last week of June and building up again the first week of July. The variation in the total counts on Sugarloaf Island following the late June peak in all three years of the study can be explained in part by the haulout patterns of parturient cows described earlier. The cows leaving the rookery on feeding trips during the first two weeks of June had little effect on the total counts due to the continual arrival of new cows to the rookery. After the population reached its plateau in mid-June, however, the cows leaving the rookery to feed were reflected in lower total counts. Pregnant cows continued to arrive at the rookery throughout the first week of July, as indicated by the birth of pups, but they added little to the total number of sea lions counted on the rookery during this time.

The total number of cows present on Sugarloaf Island during the breeding season was much lower in 1979 than in 1978, but this was not the case for the territorial bulls. The number of territorial bulls was

consistent in all three years, hence they formed a higher proportion of the total population in 1979 than in 1978.

The low variation in the numbers of bulls present on the rookery does not necessarily mean that this portion of the population did not turnover during the breeding season. Individual territorial bulls were present on Sugarloaf Island for varying lengths of time. Once a bull departed, however, it usually was replaced immediately by another bull. As the season progressed into early July, the vacated territories were either filled by younger bulls or taken over by a neighboring bull.

Young bulls were present on Sugarloaf Island in low but variable numbers throughout the breeding season. For most of that time, they were restricted to areas of the island where no breeding was taking place. They did not hold territories until the end of the breeding season. Of the four areas that were not used for breeding purposes, only two (areas 9A and 10A) were used as haulouts by nonbreeding animals. Observations of these areas and counts of the numbers of sea lions present on them from day to day showed that this segment of the population was very transient. Some recognizable individuals were resighted several times at intervals ranging from 1 to 3 days, but some recognizable individuals were never resighted. Occasionally, groups of young bulls arrived overnight and remained for less than a day, which suggested that they were travelling through the area as a group, using Sugarloaf Island as a resting area. This contrasts somewhat with what

Gentry (1970) found on Ano Nuevo Island. He states that the non-breeding bulls tended to arrive on the rookery earlier and remain longer than did the territorial bulls. As an age class, this is also true for Sugarloaf Island but it was not true for individual animals.

Juvenile sea lions were present on the Sugarloaf Island rookery in very low numbers throughout the breeding seasons of all three years of the study. These usually were associated with cows. Yearlings were present in higher numbers than the 2-4 year olds, and they generally were tolerated to a higher degree on the breeding areas. Juveniles generally were not found on those areas used by non-breeding bulls.

Although the overall numbers of sea lions utilizing Sugarloaf Island both as a haulout and as a rookery were lower in 1979 than in 1978 or 1980, the timing of events throughout the breeding season was very similar in all years. The changeover from a haulout to a rookery, as indicated by the increase in cows, occurred during the third week of May in both 1978 and 1979, and the increase in the number of cows took place within a few days of the same date in all years.

A high degree of synchrony in the peak of pupping and breeding at specific rookeries has been reported for the Steller sea lion throughout its range (Scheffer 1945, Pike and Maxwell 1958; Thorsteinson and Lensink 1962; Gentry 1970; Sandegren 1970; Mate 1973; Calkins and Pitcher 1982). Gentry (1970) reported the peak of pupping to be around the middle of June each year at the Ano Nuevo rookery in California.

Sandegren (1970) reported dates of 12-15 June for the peak of pupping at Lewis Island in Prince William Sound. Previous studies at Marmot Island revealed dates of 12 to 15 June for the peak of pupping (ADF&G unpublished data). At Sugarloaf Island the peak of pupping occurred slightly later (15-19 June) in all three years of this study.

The end of the breeding season of the Steller sea lion in the Gulf of Alaska occurs sometime in July. There is no single event that occurs to indicate the end of the breeding season, as there is for the onset of the breeding season (i.e., the occurrence of first surviving pups). Gentry (1970), Sandegren (1970) and Gisiner (1985) describe behavioral events, such as the departure of territorial bulls and their subsequent replacement by younger bulls and the decrease in pupping and number of copulations as indicators of the close of the breeding season. Gentry (1970) also mentions the return of juveniles to the rookery after the breeding season. On Sugarloaf Island, several events occurred that signaled the end of the breeding season.

In 1980, the total numbers of sea lions increased to a seasonal high in mid-July, with variable but high counts recorded until the end of the month. When the composition of this increase was examined in detail, cows were found to make up most of it; the rest was made up by young bulls and juveniles. The overall proportion of cows fell, however, from 88 percent in late June to less than 80 percent by the end of July. An equivalent rise in the proportions of young bulls and

juveniles took place during that time.

When the juvenile component was examined further, based on the sightings of known aged branded animals, it was apparent that at least a portion of these were 4 year olds. There was also an increase in the numbers of 5 year olds in late July.

Reproductive information from collected animals has indicated that some female Steller sea lions are reproductively mature at four years of age (Pitcher and Calkins 1981). This was confirmed by my observations of known-aged, branded females, which were first observed with pups in 1980, when they were five years old.

The increase in juveniles, some of which were four-year-old cows, and the arrival of previously unseen five-year-old cows in late July, may be an indication that these animals were arriving at the rookery late in the year to breed for the first time. No copulations were seen, but inasmuch as observations were not made around the clock, these could have been easily missed. If these cows were being bred at Sugarloaf Island in late July and early August, however, they were being bred by the young, subdominant bulls, for all of the dominant territorial bulls had left the island by this time.

Gisiner (1985) however saw copulations of "young looking" females without pups, as well as 2 branded 4 year olds, prior to 25 June on the Marmot Island rookery. Sandegren (1970) also reported that presumably

nulliparous females were copulating early in the breeding season at Lewis Island. Nulliparous females in other otariids are known to breed prior to females with pups, as in the southern fur seals, Arctocephalus spp. (Stirling 1971; Bonner 1981).

A change in the age structure of the population was not the only change which marked this time of the year. The position of the animals on the areas changed dramatically during the last two weeks of July and into early August. There was a general movement of animals from the higher reaches of the rookery down toward the water line, and areas previously unused by sea lions were being used extensively as haulouts.

Marmot Island

The numbers of sea lions utilizing the Marmot Island study area during the breeding season in 1979 showed extreme day-to-day variation. The variation was somewhat greater, and the numbers were lower, prior to 5 June than after that date.

The variation can be explained in part by looking at the sex and age structure of the population. Cows and juveniles comprised 90% of the population during the breeding season, and accounted for nearly 100% of the variation. Territorial bulls and young bulls were present in low but consistent numbers.

The variation may have been due to the diurnal haulout patterns of cows. New cows may have been arriving at the rookery, but not in large enough numbers to obscure the haulout patterns of those cows already present. This may explain (in part) the variation seen in the numbers of cows, but it does not explain the variation in numbers of juveniles.

Juveniles also may have exhibited a diurnal haulout pattern, but there is no reason to assume that they did, unless they were all associated with cows and followed their same patterns. Analysis of the possible correlations of numbers between juveniles and cows do not support such a relationship. Juveniles also did not have any reason to remain on the rookery for any specific length of time (as do cows, e.g., to nurse pups and to breed). Neither do they have any reason to return to the rookery within any specific length of time. A juvenile's energy requirements and feeding rythm may also be very different from a cow's.

Comparisons of populations on Sugarloaf and Marmot Islands

When the breeding season populations of Sugarloaf Island and Marmot Island are compared, several differences are readily apparent. The dramatic increase in cows that was strongly expressed in late May to early June at Sugarloaf Island was only slightly apparent at Marmot Island. Presumably, this is due to the fact that Sugarloaf Island is used very little as a haulout by non-breeders during the breeding

season, whereas Marmot Island is used as a haulout by much greater numbers of juvenile sea lions at that time. The increase in cows during the breeding season at Marmot Island therefore, is not as apparent as it is on Sugarloaf Island.

The presence of large numbers of juvenile animals on the Marmot Island rookery during the breeding season is perhaps the most striking difference from Sugarloaf Island. One possible explanation for this is that juvenile animals on Marmot Island are more closely associated with cows on the rookery than they are on Sugarloaf Island. There is some evidence to support this, in that adult cows have been observed nursing juveniles far more often on Marmot Island than on Sugarloaf Island (ADF&G unpubl. data; this study). This, however, does not explain the absence of the animals on Sugarloaf Island. I believe the topography of the two rookeries has a great deal to do with the presence/absence of juvenile animals.

The topography of the Marmot Island rookery is more conducive to the presence of juveniles than is that on the Sugarloaf Island rookery. The areas used for breeding on Sugarloaf Island are mostly above the high tide line and are, therefore, rather steep-sided, dropping off precipitously into the water. While this is not necessarily difficult terrain for a sea lion to negotiate, it is disadvantageous for juvenile animals that are harrassed and chased by both territorial bulls and adult cows, as soon as they climb onto the area. The Marmot Island

rookery, conversely, is mostly composed of long, flat beaches that afford much easier access to the rookery than on Sugarloaf Island. Many juvenile sea lions at Marmot Island were seen to surf into the periphery of the rookery and either make dashes through the area and be chased back to sea or congregate in areas temporarily vacated by cows and territorial bulls. During certain tide stages and under certain weather conditions, juvenile animals had a far greater chance of entering the rookery safely at Marmot Island than they did at Sugarloaf Island (see behavior section).

BEHAVIOR

The topography of the Sugarloaf Island and Marmot Island rookeries not only affects the sex and age structure of the population, but also has a large impact directly and indirectly on the behavior of the sea lions during the breeding season. Indirectly, the topography of the two islands determines to what extent the tidal fluctuations affect the rookery areas, and this, in turn, determines the movement patterns of the sea lions as well as the frequency of behaviors. The rookery topography also directly affects the types of territories established by breeding bulls and the stability of territorial boundaries.

Tidal fluctuations in the northern Gulf of Alaska are large, and ranged from -1.37 meters to 5.03 meters during the course of this study. The effect that these extreme tides had on the Sugarloaf Island and Marmot Island rookeries was very different and related directly to the topography of the two islands.

Most of the rookery areas on Sugarloaf Island are above the high tide line and, therefore, are not physically affected by the tide. This fact was reflected in the distribution and movement patterns of the cows. Cows on Sugarloaf Island tended to remain within several meters of where they pupped for about a week. Thereafter, during periods of hot weather, and feeding trips to sea, they would leave their pup in the same general area and go to sea.

In contrast to Sugarloaf Island, the rookery beaches of Marmot Island are comparatively flat, and subject to extreme changes in size as a consequence of rising and falling tides. The flat, unobstructed nature of the Marmot Island beaches adds to the ease with which all of the animals there can move about. Whereas cows on Sugarloaf Island tended to remain for a least a week in the same area where they gave birth and to return to that same area (and their pup) after each feeding trip, cows on Marmot Island were much more mobile. In periods of hot weather, they were seen to carry their pups down to areas of wet sand, near the tideline. Cows on Marmot Island also placed their pups high on the beach upon leaving the rookery for feeding trips.

Edie (1977) determined that a cow's location and movement over the rookery at Cape St. James was determined by several factors, including ease of access from the water, protection from waves, ruggedness of terrain and availability of water. Gentry (1970) and Gisiner (1985) also found that the availability of water for thermoregulation was important in the distribution of cows at Ano Nuevo Island. During the 1981 study on Marmot Island, the cows were consistently at the water's edge during periods of hot weather. This was not found to be true on Sugarloaf Island, where cows tended to leave the rookery areas completely during periods of hot weather. The tides and weather, therefore, had a direct impact on the cows' distribution on the beaches of Marmot Island, whereas they had little effect on Sugarloaf Island.

Gentry (1970) and Gisner (1970) both define a territory as having stable boundaries, if those boundaries remain unchanged over a period of time. Steller sea lion bulls are known to establish territories with boundaries that follow topographic features of the substrate, such as cracks, boulders and terraces (Gentry 1970). The Sugarloaf Island rookery is typical of this type of habitat. The territorial bulls of Sugarloaf Island used the topography extensively in establishing the boundaries of their territories, with virtually every shared boundary of a territory following some sort of topographic feature. The territories therefore, usually did not change in shape or size during the breeding season. When new territories were established, their boundaries also followed topographic features of the terrain.

The two types of territories on the Sugarloaf Island study area, landlocked and water, are the result of the stability of the boundaries and lack of the effect of tides. A bull's territory, once established, did not change in relation to its proximity to the water.

In contrast, the Marmot Island study area had almost no topographic relief. On the flat, sandy beaches, the bulls, therefore, did not have the benefit of topographic features, along which they could establish territorial boundaries. The result was that the boundaries were rather ambiguous on Marmot Island, with territories constantly changing in shape and size.

The three types of territories on Marmot Island (landlocked, tidal and semiaquatic) are therefore, products of the tide. Bulls in landlocked territories remained close to the cliff at all tidal stages, and were prevented from gaining access to the water (without abandoning their territory) by the presence of the bulls in tidal territories ("tidal bulls"). The tidal bulls are positioned along the water's edge, with their territories extending up the beach into unwashed sections, as well into the surf line. These bulls constantly change their position to follow the water line. The semi-aquatic territories are patrolled by bulls in the area of the beach that is constantly awash by waves. At high tides, these bulls are totally aquatic, at low tides they are just at or below the water line. This differs somewhat from the result that Gisiner (1985) reported for Marmot Island. He defined two types of

territories; those established along the tide line, and those landward of the tide line. He classified all other bulls as "peripheral" bulls and did not include them in his study.

Other studies of Eumetopias have shown that the types of territories are influenced by the topography. Sandegren (1970) noted three types of bulls on the rocky substrate of Lewis Island, peripheral bulls located above and below the tide line, and semiaquatic bulls with territories along the tide line. Sandegren (1970) also mentioned, however, that even though the bulls would move in relation to the tide within their territories, their territorial boundaries were stable. Presumably, this has to do with the rocky substrate of the Lewis Island rookery.

The differences in topography and the associated differences in the population structure, tidal effects and territory stability on the Sugarloaf Island and Marmot Island rookeries also are reflected in the territorial behavior of the bulls at each island. The two rookeries were compared on the basis of male territorial behavior, using the durations of the bulls on the territories, juvenile chases, territorial displays and the copulation success of the bulls. Internal differences within each rookery were investigated for these same behaviors on the basis of territory type and tide stage.

Territorial bulls on Sugarloaf Island and Marmot Island follow the same pattern of arrival and departure (and subsequent replacement by other bulls) as has been described for Steller sea lion bulls at Ano Nuevo Island in California (Gentry 1970; Gisiner 1985). The mean duration of the territorial bulls' residence on their territories at Sugarloaf Island (27 days) and Marmot Island (22 days) are shorter than the 35 to 40 days described by Gentry (1970) for territorial bulls at the Ano Nuevo rookery. The difference in the duration of bulls on Marmot Island from those on Sugarloaf Island might be due to the differences in the types of territories found on the two islands.

The first bulls departed the Marmot Island rookery 13 days before the departure of the first bulls from the Sugarloaf Island rookery. Complete replacement of original bulls had taken place on Marmot Island by 5 July, 12 days earlier than on Sugarloaf Island. Overall, bulls on the Sugarloaf Island rookery may have a lower expenditure of energy in maintaining their territories than the bulls on Marmot Island, due to the greater stability of their territories. This may be the cause of the longer durations of the Sugarloaf Island bulls.

Gisiner (1985) found that bulls abandon their territories earlier at Marmot Island than at Ano Nuevo Island. On Marmot Island over 50 percent of the bulls abandoned their territories by 30 June, whereas at Ano Nuevo Island less than 4 percent had left before 1 July. Gentry (1970) attempted to measure the relationship between territory size,

frequency of boundary displays, and duration of defense for bulls at Ano Nuevo Island, but could not find any simple relationship.

Because the terrain at Sugarloaf Island is not conducive to occupation by juvenile animals during the breeding season, the frequency of occurrence of chases of this age class by territorial bulls is low there at both high and low tides. At Marmot Island, however, the frequency of chases of juvenile animals was high and certainly related to the abundance of these animals on the breeding areas. Access to the rookery was much easier for juveniles at Marmot Island than at Sugarloaf Island, because of the flat, unobstructed nature of the beaches. The higher frequency of chases at low than at high tides appears to have been partly a function of the greater area of beach available at low tide. Juvenile animals were more likely to make forays onto the beach at low tides, when the animals on the beach were more widely dispersed, than at high tides, when the animals were more closely packed.

Gisiner (1985) also found that maximum intrusion rates by juveniles were higher at low tides on the Marmot Island rookery. In comparisons with the Ano Nuevo rookery however, he found that although the juvenile population was much higher at the Marmot Island rookery, compared with Ano Nuevo, the intrusions by juveniles into the rookery were lower than at Ano Nuevo. He attributed this to the topography, stating that the beaches of Marmot Island did not afford the juveniles the same opportunity to approach the rookery undetected as the sloping rocky

terrain at the Ano Nuevo rookery. I feel that the converse is true when Marmot Island is compared to Sugarloaf Island. The flat, unobstructed beaches of the Marmot Island rookery afforded juveniles much easier access to the rookery areas than did the steep slopes and outcrops of the Sugarloaf Island rookery.

On the Sugarloaf Island rookery tides had very little effect on the frequency of territorial displays. At Marmot Island, however, the frequency of territorial displays between bulls was much greater at high tides than at low tides. Territorial displays on Marmot Island seemed to be related to the position of the cows and the spacing of the bulls, rather than to any set territorial boundary. The distance between the bulls decreased as the tide rose, coinciding with an increase in the frequency of their displays. The frequency of the displays during low tide at Marmot Island did not differ significantly from the frequency of displays at Sugarloaf Island.

Even though the Sugarloaf Island and Marmot Island rookeries were found to be different in their population structure and territorial systems, the copulation success of the bulls did not differ significantly between the islands. The tide, while having a great effect on the territorial behavior of the bulls on Marmot Island, did not seem to affect the copulation success of the bulls overall.

In polygynous pinnipeds, the establishment and maintenance of a territory by males allows them access to females for breeding purposes (Bartholomew 1970; Miller 1975; Stirling 1975). However, not every male that succeeds in establishing a territory gains access to or successfully breeds with females on the rookery (Gentry 1970; Sandegren 1970, Miller 1975, Gisiner 1985). Gentry (1970) found that only 63 percent (14) of the territorial bulls on Ano Nuevo Island copulated, and that 50 percent of the successful males achieved 87 percent of the copulations. Sandegren (1970) also found males copulating in disproportionate frequencies. Presumably, the difference in the reproductive success of individual males is due to the location of their territory on the rookery, in relation to the distribution of females (Gentry 1970).

The distribution of cows over the study areas of Sugarloaf Island and Marmot Island was considerably different. On Sugarloaf Island where the cows were distributed more or less evenly over the available area, the location of a bull's territory (landlocked or water) was unrelated to the frequency of displays, juvenile chases or copulations. In addition, no difference was found between the males on landlocked or water-access territories at either high or low tides which reflects lack of tidal influence at Sugarloaf Island. On Marmot Island, however, the tide and weather do greatly influence the distribution of cows and bulls over the area. At low tide, there was no difference in the frequency of displays or chases between the bulls on the different types of

territories (landlocked, tidal and semiaquatic). However, at high tide bulls in landlocked territories chased juveniles more often than did bulls in semiaquatic territories. Bulls in tidal territories also displayed more than bulls in landlocked or semiaquatic territories at high tide.

The fact that bulls on landlocked territories displayed just as frequently as those on tidal territories is somewhat surprising, in that one would expect landlocked bulls to display less at low tide, especially because the females and the tidal bulls tended to move away from them with the tide. The intrusion of juvenile males onto the rookery, however, is high at low tides and landlocked bulls may have been displaying to one another after chasing juveniles out of their territories. On Marmot Island, territorial displays seemed to occur as a result of a bull's proximity to another bull rather than to a physical boundary. Perhaps, the chases of juvenile animals brought bulls closer together in certain instances, thereby resulting in territorial displays that otherwise would not have taken place.

The frequency of copulations at low tides was consistent with the location of the tide and the cows. Tidal bulls copulated significantly more often than landlocked or semiaquatic bulls at low tides. One might expect the semiaquatic bulls to copulate more frequently at low tides than the landlocked bulls, considering the position of the females. The close proximity of the tidal bulls, however, may have prevented them

from doing so.

Tidal bulls displayed significantly more at high tide than either semiaquatic bulls or landlocked bulls. This is also somewhat surprising in that one would expect landlocked bulls to display most during periods of high tides. The results, however, may indicate that tidal bulls are displaying to both semiaquatic and landlocked bulls, while landlocked bulls are only displaying to tidal bulls and other landlocked bulls.

Copulation frequencies at high tides again reflect the position of the females, in that landlocked and tidal bulls copulated significantly more often than semiaquatic bulls. At high tides, the distribution of the females is more likely to range from the tide line toward the cliffs, thus many more cows are in the landlocked bulls' territories than at the lower tide stages.

There is some disagreement in the literature as to whether bulls defend territories in the absence of females. Gentry (1970) indicated that bulls at Ano Nuevo Island did establish territories in areas that were not utilized by females, however he did not know how continuous the territorial maintenance was. Sandegren (1970) maintains that bulls at Lewis Island did not establish territories in the absence of females.

On Sugarloaf Island, a majority of the bulls arrive and establish territories before the arrival of the cows. Some of these bulls occupy territories which, for one reason or another, never become used by cows.

The duration of these bulls' occupancy of vacant territories, however, is not known.

On Marmot Island, some landlocked and semiaquatic bulls definitely defended territories in the absence of cows throughout the breeding season in 1981. These bulls were, for the most part, deprived of cows because of the tide and the weather. The weather in 1981 was exceptional, in that it was calm and sunny for six weeks, from the end of May to the first part of July. This fair weather combined with a lack of storms at sea (therefore a lack of storm tides), effectively keeping the cows at or very near the tideline throughout the breeding season and out of the territories of some of the landlocked bulls. The typical weather pattern for this part of the Gulf of Alaska is one of rain and fog, with storms from the southeast. Since the breeding beaches of Marmot Island face due east, that typical weather brings wind-driven waves onto the beaches, reducing the rookery to only a narrow strip between the cliffs and the high tides. This definitely would change the distribution of the cows, and probably increase the access of landlocked bulls to the females.

In 1981, the bulls' durations of occupancy on the landlocked, tidal and semiaquatic territories were not significantly different from one another. I suggest that landlocked bulls, while probably never as successful as tidal bulls, would be more successful in years of inclement weather than good weather. Since inclement weather is the

usual weather pattern, landlocked bulls would benefit by waiting for a change in weather, rather than to abandon their territories in the absence of cows.

Semiaquatic bulls were the least successful bulls on the rookery in 1981. The few copulations by semiaquatic bulls were with cows that were either leaving or entering the rookery. In certain instances, peripheral bulls on a rookery may have a limited degree of reproductive success if their territories are adjacent to movement corridors of cows leaving or returning to the rookery (Gentry 1970; Edie 1977). On Marmot Island, cows can leave and return to the rookery at any point along the beach. Peripheral bulls, therefore, cannot "choose" preferred movement corridors of cows but can only patrol the outer reaches of the beach, waiting for any cows that may be in estrus to enter or leave the rookery through their territories.

SUMMARY AND CONCLUSIONS

Sugarloaf Island and Marmot Island are the largest Steller sea lion rookeries in the northern Gulf of Alaska, producing approximately 40 percent of the pups in that area annually. The two rookeries also differ radically in their substrate properties. Marmot Island is the only rookery in the northern gulf where sea lions haulout and breed on

sandy beaches. Sugarloaf Island is composed of boulders and rocky outcrops, which is typical of other rookeries in the Gulf. This study was designed to determine the influence of rookery terrain on the population structure and territorial behavior and breeding success of male Steller sea lions on two physiographically different rookeries in the Gulf of Alaska.

Total counts, sex and age composition counts and counts of known-aged branded animals were conducted on Sugarloaf Island in 1978, 1979 and 1980. These counts were compared to similar counts made on Marmot Island in 1979. Information on the behavior of territorial bulls was collected at Sugarloaf Island in 1980 and Marmot Island in 1981. In order to assess the influence of the tide on the behavior of territorial bulls at the two rookeries a sampling scheme was designed around high and low tides.

Sugarloaf Island was used by varying numbers of sea lions of both sexes and all ages (except adult males) during the prebreeding season. Daily and yearly variation was found in the numbers of sea lions utilizing Sugarloaf Island during the prebreeding season.

During the breeding season the Sugarloaf Island rookery was used by adult cows and territorial bulls for breeding and pupping with variable, but lower, numbers of young bulls and juveniles. The Marmot Island rookery also was used by adult cows and territorial bulls with low numbers of young bulls, as was Sugarloaf Island. The juvenile component

of the population on Marmot Island during the breeding season, however, was much higher and more variable than it was on Sugarloaf Island.

Higher numbers of juvenile animals utilized Sugarloaf Island during the postbreeding season than during the breeding season. The low numbers of juveniles on Sugarloaf Island during the breeding season (and higher numbers of juveniles on Marmot Island) may be related to the rookery terrain of the two islands. The flat, sandy beaches of Marmot Island afford the juveniles easier access to the rookery areas than the steep slopes and cliffs of Sugarloaf Island.

The behavior of territorial bulls also was different between the two Islands. Two types of territories were maintained by bulls on Sugarloaf Island: landlocked territories and territories with access to the water. Territorial bulls utilized three types of territories on Marmot Island; landlocked, tidal and semiaquatic. The boundaries of territories on Sugarloaf Island were stable, followed topographic features of the substrate and were unaffected by the tide. On Marmot Island, territory boundaries were unstable, their positions shifting with the tide.

Within Marmot Island, the territorial behavior of the bulls differed depending on the tide stage. Territorial bulls on Marmot Island chased juveniles more often at low tides than at high tides, and displayed more often at high tides than at low tides. The frequency of copulation, however, was similar at low and high tides. On Sugarloaf

Island no difference was found in the frequency of behaviors at low tide when compared to high tide.

The behavior of the territorial bulls on Sugarloaf Island was compared to the behavior of the territorial bulls on Marmot Island. Territorial bulls chased juveniles at high and low tides significantly more on Marmot Island than on Sugarloaf Island. Territorial displays at high tide were significantly greater on Marmot Island than on Sugarloaf. There was no difference in the frequency of displays between the two islands at low tide. There also was no difference in the frequency of copulations observed between the two islands at high or low tides.

The behavior of territorial bulls occupying different types of territories was compared within each of the islands at low tide and high tide. There was no difference in the frequency of chases, displays or copulations between bulls in landlocked territories and bulls in territories with access to water at any tide stage on Sugarloaf Island. On Marmot Island significant differences in the frequency of behaviors at the different tide stages were found among the bulls occupying the three different territories (landlocked, tidal and semiaquatic).

At high tide, bulls in landlocked and tidal territories chased juveniles more often than bulls in semiaquatic territories. Bulls in tidal territories also displayed more than bulls in landlocked or semiaquatic territories at high tide. Bulls in landlocked and tidal territories copulated more frequently at high tide than did semiaquatic

bulls.

At low tide there was no difference in the frequency of chases or displays between any of the bulls occupying the three different types of territories on Marmot Island.

Territorial bulls on Marmot Island left the rookery at an early date than the bulls on Sugarloaf Island. Within Sugarloaf and Marmot Island no difference was found in the duration of occupancy for bulls in the different types of territories.

The most obvious difference between the Marmot Island and Sugarloaf Island rookeries is their topography. This topographical difference, I believe, is the major cause for the difference in the sex and age structure of the sea lion populations using the two islands during the breeding season. The topography also influences the extent to which tides and weather affect the rookery areas of each island, and it is a factor in the stability of territorial boundaries of bulls.

As a result of the tidal influence and lack of topographic features on Marmot Island, the territorial system is not as stable as it is on Sugarloaf Island, where tides have little effect and territorial boundaries follow topographic features of the substrate.

The less stable territorial system on the Marmot Island rookery, combined with the presence of many juvenile animals, coincided with territorial bulls displaying more often and chasing juveniles more often on Marmot Island than on Sugarloaf Island.

The difference in the topography of the two islands, and the resulting differences in the territorial systems of the bulls, was unrelated to the overall breeding success of the bulls on the two islands. The breeding success of bulls on the Marmot Island rookery, however, depended upon the location of their territories relative to the tide and the location of females. This was not the case on Sugarloaf Island.

LITERATURE CITED

Bailey, E.P. 1976. Breeding bird distribution in the Barren Islands, Alaska. Murrelet 57:212.

Bartholomew, G.A. 1970. A model for the evolution of pinniped polygyny. Evolution 24:546-559.

B.M.D.P. 1981. Biomedical statistical software. University of California, Los Angeles, CA. 725 pp.

Bonner, W.N. 1981. Southern fur seals-Arctocephalus. In: S.H. Ridgway and R.J. Harrison (eds). Handbook of marine mammals. Academic Press, New York, N.Y. pp. 161-208.

Calkins, D.G. and K.W. Pitcher. 1977. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. In: Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1977, Vol. 1. Receptors-Mammals. pp. 433-502.

Calkins, D.G. and K.W. Pitcher. 1978. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. In: Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1978, Vol. 1. Receptors-Mammals. pp. 371-386.

Calkins, D.G. and K.W. Pitcher. 1979. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. In: Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1979, Vol. 1. Receptors-Mammals. pp. 144-208.

Calkins, D.G. and K.W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Alaska Department of Fish and Game. Anchorage, AK. 129 pp.

Conover, W.J. 1980. Practical nonparametric statistics. John Wiley and Sons, New York, NY. 493 pp.

Edie, A.G. 1977. Distribution and movements of Steller sea lion cows (Eumetopias jubatus) on a pupping colony. M.S. thesis. University of British Columbia, Vancouver, B.C. 80 pp.

Fiscus, C.H. 1961. Growth in the Steller sea lion. J. Mammal. 42:218-223.

Fiscus, C.H. and G.A. Baines. 1966. Food and feeding behavior of Steller and California sea lions. J. Mammal. 47:195-200.

Gentry, R.L. 1970. Social behavior of the Steller sea lion. Ph.D. dissertation. University of California, Santa Cruz, CA. 113 pp.

Gisiner, R.C. 1985. Male territorial and reproductive behavior in the Steller sea lion, Eumetopias jubatus. Ph.D. dissertation. University of California, Santa Cruz, CA. 146 pp.

Kenyon, K.W. 1962. History of the Steller sea lion at the Pribilof Islands, Alaska. J. Mammal. 43:68-75.

Kenyon, K.W. and D.W. Rice. 1961. Abundance and distribution of the Steller sea lion. J. Mammal. 42:223-234.

LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14:163-176.

Loughlin, T.R., D.J. Rugh, and C.H. Fiscus. 1984. Northern sea lion distribution and abundance: 1956-1980. J. Wildl. Manage. 48:729-740.

Manuwal, D.A. 1977. Dynamics of marine bird populations on the Barren Islands, Alaska. In: Environmental Assessment of the Alaskan Continental Shelf, Annual Reports of Principal Investigators for the year ending March 1977, Vol. IV. Receptors-Birds. pp.245-420.

Mate, B.R. 1973. Population kinetics and related ecology of the northern sea lion, Eumetopias jubatus, and the California sea lion, Zalophus californianus, along the Oregon coast. Ph.D. dissertation. University of Oregon, Eugene, OR. 93 pp.

Mathisen, O.A. 1959. Studies on Steller sea lions (Eumetopias jubata) in Alaska. Trans. N. Am. Wildl. Conf. 24:346-356.

Mathisen, O.A., R.T. Baade, and R.J. Lopp. 1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43:469-477.

Mathisen, O.A. and R.J. Lopp. 1963. Photographic census of the Steller sea lion herds in Alaska, 1956-1958. U.S. Fish and Wildlife Service Special Scientific Report-Fisheries No. 424. Washington, D.C. 20 pp.

Miller, E.H. 1975. Social and evolutionary implications of territoriality in adult male New Zealand fur seals, Arctocephalus fosteri (Lesson, 1828), during the breeding season. Rapp. p.-v. Reun. Cons. int. Explor. Mer 169:170-187.

Neter, and Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc. Homewood, IL. 842 pp.

Nishiwaki, M. and F. Nagasaki. 1960. Seals of the Japanese coastal waters. Mammalia 24:459-467.

Orr, R.T. and T.C. Poulter. 1967. Some observations on reproduction, growth and social behavior in the Steller sea lion. Proc. Calif. Acad. Sci. 35:193-226.

Peterson, R.S. 1968. Social behavior in pinnipeds with particular reference to the northern fur seal. In: R.J. Harrison, et al. (eds). The behavior and physiology of pinnipeds. Appleton-Century Crofts, New York, NY. pp. 3-53.

Peterson, R.S. and G.A. Bartholomew. 1967. The Natural history and behavior of the California sea lion. Spec. Publ. Amer. Soc. Mammal. 79 pp.

Pike, G.C. 1961. The northern sea lion in British Columbia. Canadian Audubon 23:1-15.

Pike, G.C. and B.E. Maxwell. 1958. The abundance and distribution of the northern sea lion (Eumetopias jubata) on the coast of British Columbia. J. Fish. Res. Bd. Canada 15:5-17.

Pitcher, K.W. and D.G. Calkins. 1981. Reproductive biology of Steller sea lions in the Gulf of Alaska. J. Mammal. 62:599-605.

Rowley, J. 1929. Life history of the sea lions on the California coast. J. Mammal. 10:1-39.

Sandegren, F.E. 1970. Breeding and maternal behavior of the Steller sea lion (Eumetopias jubata) in Alaska. M.S. thesis. University of Alaska, Fairbanks, AK. 138 pp.

Scheffer, V.B. 1945. Growth and behavior of young sea lions. J. Mammal. 26:390-392.

Sokal, R.R. and F.J. Rohlf. 1969. Introduction to biostatistics. W.H. Freeman, San Francisco, CA. 368 pp.

Spalding, D.J. 1964. Comparative feeding habits of the fur seal, sea lion and harbour seal on the British Columbia coast. Fish. Res. Bd. Canada Bull. 146. 52 pp.

Stirling, I. 1971. Studies on the behavior of the south Australian fur seal, Arctocephalus forsteri (Lesson). Austr. J. Zool. 19:243-273.

Stirling, I. 1975. Factors affecting the evolution of social behavior in the Pinnipedia. Rapp. p.-v. Reun. Cons. int. Explor. Mer 169:170-187.

Tikhomirov, E.A. 1959. The question of the use of warm blooded animals as food by sea lions. Izvestiia TINRO 47:185-186.

Tikhomirov, E.A. 1964a. Distribution and hunting of the sea lion in the Bering sea and adjacent parts of the Pacific. In: P.A. Moiseev (ed.), Soviet Fisheries Investigations in the Northeast Pacific 3:281-285.

Tikhomirov, E.A. 1964b. Distribution and biology of pinnipeds of the Bering Sea. In: P.A. Moiseev (ed.), Soviet Fisheries Investigations in the Northeast Pacific 3:272-280.

Thorsteinson, F.V. and C.J. Lensink. 1962. Biological observations of Steller sea lions taken during an experimental harvest. J. Wildl. Manage. 26:353-359.

Wilke, F. and K. Kenyon. 1952. Notes on the food of the fur seal, sea lion and harbor porpoise. J. Wildl. Manage. 16:396-397.

Vania, J. and E. Klinkhart. 1967. Marine mammal report. Ann. Segment Rept. Fed. Aid Wildl. Restoration, Alaska Department of Fish and Game, Juneau. Vol. VIII. 24 pp.